

CURRENT-INDUCED FLOW THROUGH THE SPONGE, *HALICHONDRIA*

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The entire phylum Porifera consists of suspension-feeding organisms, simple by comparison with other multicellular animals, but nonetheless highly specialized for separating small organisms and other nutritive particulate matter from the water passing through themselves. A sponge, in Bidder's (1923, page 312) felicitous phrases, is "a mere living screen between the used half of the universe and the unused half—a moment of active metabolism between the unknown future and the exhausted past."

As Grant (1825) first showed, water passes unidirectionally through an elaborate system of pores, gates, and canals and, following filtration, is returned to the medium from which it was drawn. This flow of water through sponges has been regarded as being due entirely to the activity of certain peculiar flagellated cells, the choanocytes. Indeed, early workers such as Grant (1825) and Bowerbank (1864) devoted considerable ingenuity to demonstrations that muscles played no role.

And the general design of sponges is consistent with the requirements for a substantial output—one of Bidder's (1937, pages 129) *Leuconia aspera* Schmidt "threw, to a distance of 70 cm, 1000 times its own bulk of water per hour"—from a pump consisting of uncoordinated cells. Flagellated chambers with a combined cross-sectional area many times that of the outer surface of the animal lead into a collecting manifold in which successive generations of channels are both fewer in numbers and of smaller total cross-section. Thus the velocity of the final excurrent stream through the osculum may be several hundred times that at the level of the choanocytes. The reduction in cross-section of the final common canal at the osculum has been interpreted as a further device to increase the excurrent velocity, and the oscular chimneys have been regarded as a means of increasing the distance between excurrent and incurrent openings. Both features presumably reduce the likelihood of recycling previously filtered water (Bidder, 1923; Leigh, 1971).

But this generally accepted picture may, in fact, overlook another important element propelling water through at least some sponges under certain circumstances. Previous observations of the pumping activities of sponges were made with the animals in still water (except for the field work of Reiswig, 1971). Yet sponges appear to require moving water in their normal habitats; DeLaubenfels (1954) feels that velocities of two or three kilometers per hour are optimal. This requirement has been interpreted as insuring that silt and debris do not accumulate and as further insurance against reingestion of a sponge's output. But, whatever its other functions, *the presence of a current in the medium around an attached sponge raises the possibility of flow through the animal without active pumping by the choanocytes.* Such induced flows have been termed "passive"

since they do not entail immediate metabolic cost (Vogel and Bretz, 1972). The present investigation seeks to determine whether passive flow might be an appreciable factor in the lives of sponges.

It should be noted that passive flow, while it may avoid metabolic expenditure, involves no novel source of energy. A potential exists between any two points where the velocity of the medium is different; where a potential exists, work may be extracted by an appropriate device. For an attached organism, the velocity at the point of attachment is, of course, zero; and it can extract energy from the flow of fluid around it just as does a windmill.

At least three physical mechanisms permit the induction of flow in a spongelike structure by motion of the external medium (Fig. 1). (A) If a small pipe connects two points in a larger channel, and if the ends of the small pipe are normal to the walls of the channel, then fluid will flow in the small pipe from the end where flow in the channel is slower to the end where flow is more rapid (1a). By

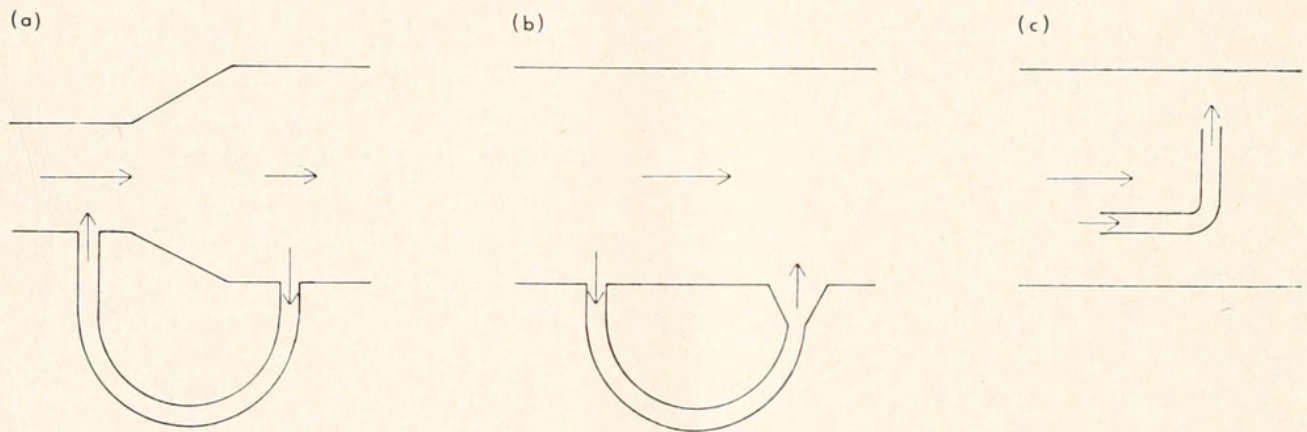


FIGURE 1. Several arrangements whereby flow in a larger channel may induce unidirectional fluid movement in a small pipe.

Bernoulli's principle, the increase in velocity in the channel is concomitant with a reduction in pressure in order that energy be conserved; this pressure difference, then, induces flow in the small pipe. The direction of flow in the channel is, of course, inconsequential. With sponges, the medium should travel fastest as it crosses the highest points, which commonly bear the oscula. Thus the internal flow will be directed from any ostia not atop a major protrusion toward any terminal oscula on the protrusions.

(B) If a small pipe terminates normal to the wall of a larger channel through which fluid is moving, then fluid will be drawn from the pipe into the channel by an additional agency, termed viscous entrainment or sucking, and caused by the resistance of real fluids to rapid shear rates. Faster movement of the fluid in the channel will produce greater rates of entrainment (1a). In addition, the rate of entrainment will depend on the size of the aperture (1b); it is to avoid errors due to entrainment that the static (normal) aperture on pitot tubes (as used for airspeed indication in small planes) must be kept small (Prandtl and Tietjens, 1934). In a finger-like or encrusting sponge, water will therefore be drawn out of a terminal osculum because, as the highest point on the structure the latter will

be exposed to the greatest velocity, as well as because the oscula are larger holes than the ostia.

(C) If a small pipe bent at a 90° angle is oriented in a moving stream so that one aperture is directed upstream and the other is normal to the stream, then fluid will enter the former and run out of the latter (1c). The normal aperture "sees" only the static pressure of the fluid; the one directed upstream is exposed to the sum of the static pressure and the additional dynamic pressure caused by the deceleration of the fluid in front of the aperture. In a finger-like sponge, an ostium directed upstream will thus be exposed to a higher pressure than will an osculum normal to the flow. If the external flow reverses direction, then ostia on the opposite side of the finger will be exposed to the higher pressure, and internal flow will still be from ostia to oscula.

For a sponge with a terminal osculum, all three mechanisms predict the same direction of flow—from ostia to oscula. It has not yet proven feasible, either by theory or measurement, to apportion the passive flow among the different mechanisms which might be responsible. One can, however, state that size, shape, and location of the openings should all be relevant to determining the direction of passive flow. Consideration of these possible physical mechanisms suggests that a good excurrent opening should be large, at the terminus of a fairly sharp projection, and farthest from the point of attachment to the substratum.

That a saving in the energy expended in filtering water might be important to sponges is evident in the calculations of Jørgensen (1966). His figures, based on filtration rates and oxygen consumption in still water, suggest that the nutritive value of the suspended material available may not greatly exceed the cost of filtration.

Passive flow makes a significant contribution to the ventilation of the burrows of prairie-dogs (Vogel, Ellington and Kilgore, 1973) and mounds of certain African termites (Weir, 1973), and it may have been crucial to the success of archeocyathids in the Cambrian (Balsam and Vogel, 1973).

Ideally, an evaluation of passive flow in sponges should be based on direct observations in nature and on a theoretical analysis of the hydrodynamics of the situation. Direct observation, however, has given ambiguous results due to the complexity and variability of the currents around the sponges investigated. And theoretical analysis has been frustrated by the complexity of the physical mechanisms involved. An operational compromise, the present investigation divides into three experimental portions: first, observation and measurements of flow through living and freshly killed sponges exposed to moving sea-water in the laboratory; secondly, measurements of flow rates through a brass model of a sponge in a flow tank; and thirdly, observations on the influence of the geometry of apertures on the induction of flow.

MATERIALS AND METHODS

Fresh material

Sponges (*Halichondria bowerbanki* Burton: see Hartman, 1958) were collected by the Supply Department of the Marine Biological Laboratory, the encrusting form near Woods Hole, Massachusetts, the more erect and finger-like

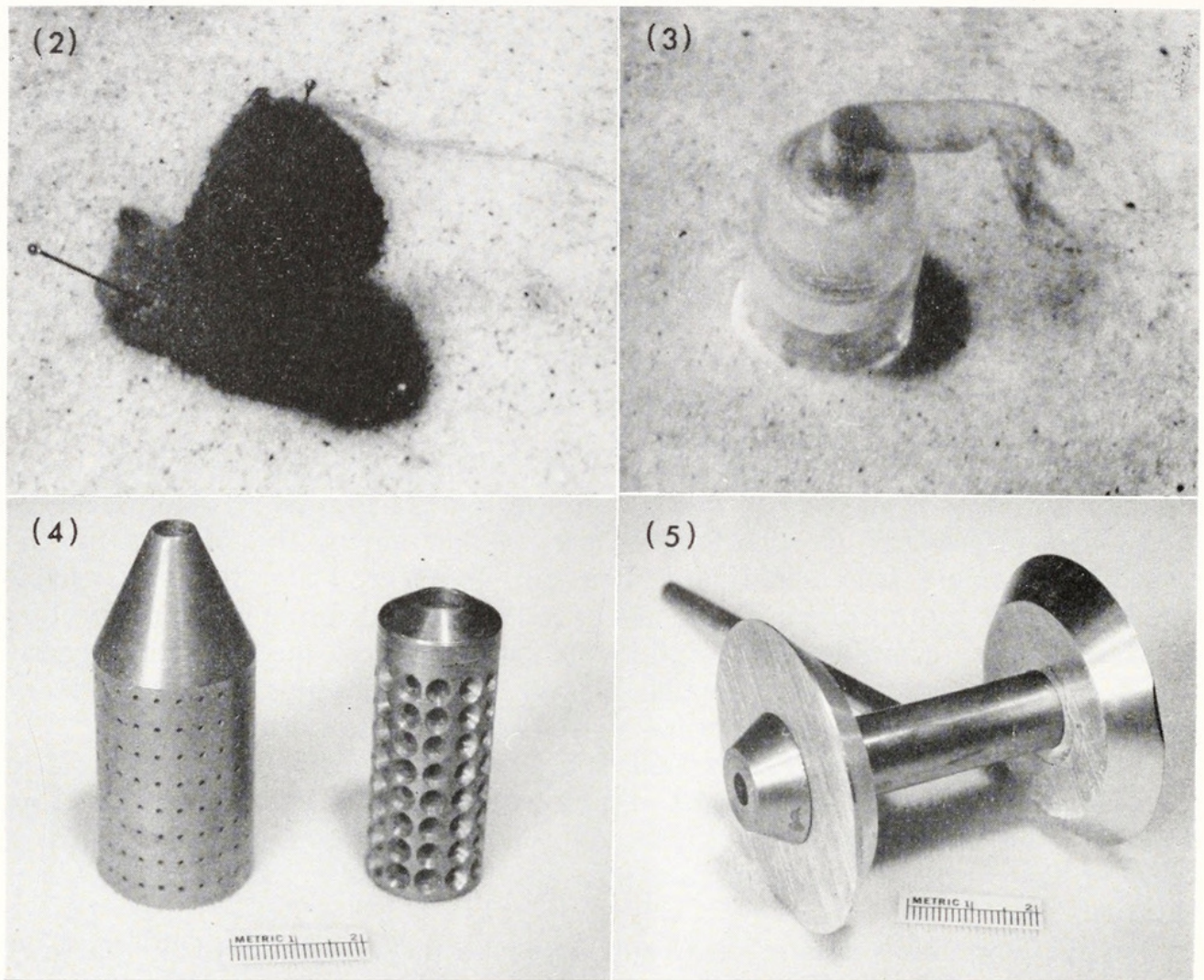


FIGURE 2. Rhodamine B passing through a freshly killed *Halichondria* at an external current of about 5 cm/sec.

FIGURE 3. Rhodamine B passing through a plexiglas model (described by Vogel and Bretz, 1972) under the same conditions as in Figure 1. The model is 2.5 cm high.

FIGURE 4. Brass model on which the data of Figure 8 were obtained. The smaller cylinder inserts into the larger through a hole in the bottom of the latter. Two of the small holes in the outer cylinder communicate with each chamber in the walls of the inner cylinder; thus holes in outer and inner cylinders are not aligned.

FIGURE 5. Apparatus for testing apertures in pairs. Each aperture is radially symmetrical and was oriented normal to the stream; dye was introduced through the small pipe, which also served as a support. Large collars on either end of the main tube reduced the sensitivity of flow through the tube to minor misalignments in the stream.

form from the Cape Cod Canal. All were maintained in running sea water and used within a day of collection. In the erect form, active pumping usually ceased within a few hours after the sponges were received, probably due to the warmer water at the laboratory.

With the addition of curved corner fairings, a sea-table, $132 \times 76 \times 10$ cm inside, provided an adequate flow tank for use with the fresh sponges. The supply hose, fixed to one wall and directed downstream, propelled water at up to 10 cm/sec. Water left through a porous cylinder fixed to the drain, thereby providing a continuously changing medium in the tank and facilitating observations of the patterns of flow with dye markers. Of several colored materials used, a concentrated

solution of rhodamine B in sea water was by far the most suitable for marking flows; in practice it was introduced from a hypodermic syringe, and it stained neither plastic models nor sponges.

"Fingers" of *Halichondria* were cut from colonies with a substantial portion of the basal portion of the colony left attached and without cutting into the axial spongocoel; these were pinned to wax in a small finger bowl. Above the wax, a small amount of sand provided convenient fairing material to obscure the cut end of the sponge and to raise the substratum to the level of the rim of the bowl (Fig. 2). After introduction into the sea table, each specimen was checked with a dye marker for active pumping; several either stopped pumping shortly thereafter or never showed evidence of pumping. Certain of the latter were used for measurements of passive flow. Active pumping, when occurring, was steady, with none of the polyrhythmic character of the ventilatory flow of, for example, burrowing polychaetes. No specimen which spontaneously stopped pumping was ever observed to start again. For most measurements of passive flow, sponges were deliberately "turned off" by immersing them in fresh water for about five minutes. Parker (1910) found that this treatment eliminated active pumping without causing constriction of either ostia or oscula in *Stylotella*. Fresh water produced no visible effects on the openings of *Halichondria*, and the performance of sponges which had spontaneously stopped pumping was indistinguishable from those treated with fresh water.

For measurements of flow inside a specimen, a probe (see below) was lowered about 4 mm below the tip of the osculum; the same probe was repositioned about 3 cm in front of the sponge to record the outside velocity. Traverses from the level of the osculum down to the sand fairing showed an essentially constant velocity—the use of a finger-bowl to hold specimens reduced the boundary-layer thickness to insignificance.

Models

Models were made from cylindrical metal or plexiglas stock on a combination lathe and milling machine.

A linear flow tank filled with fresh water was employed for measurements on all models. This device consisted of a plywood channel, $244 \times 23 \times 17$ cm, connecting two 200-liter, open cylindrical drums. A 1.5 HP centrifugal pump in the return circuit provided flow rates of about 7 l/sec or (depending on the depth of water in the channel) up to 40 cm/sec. An adjustable bypass around the pump together with an adjustable gate at the downstream end of the channel controlled the flow rate and depth in the channel. Flow was smoothed by baffling in the fore-tank and by an array of small pipes acting as a straightener at the entrance to the channel. These devices proved adequate: a blob of dye remained visually discrete as it travelled the length of the channel. More water passed through the lower portion of the adjustable gate than through the upper portion, thus compensating for the retardation caused by the floor of the channel. As a result, the speed of flow was nearly uniform from within a few millimeters beneath the surface to about a centimeter above the bottom at the place, about half-way down the channel, at which all measurements were made.

Flow-meter

Flow rates were measured with a heated-bead thermistor flow-meter (Figure 6) whose accuracy was estimated (on the basis of repeated calibrations) as ± 0.5 cm/sec between 0 and 30 cm/sec. Several limitations on the use of this instrument deserve comment. In the absence of a temperature-compensating circuit, measurements had to be made at water temperatures differing no more than 1°C from that of the calibration. The instrument had a substantially non-linear response, giving a greater change in output for a given change in flow rate at low velocities. The thermistor bead together with its glass envelope on the end of the probe was 2.0 mm in diameter while the diameter of the cylindrical shaft of the probe was 1.5 mm; thus the probe seriously occluded oscula less than about 3 mm across.

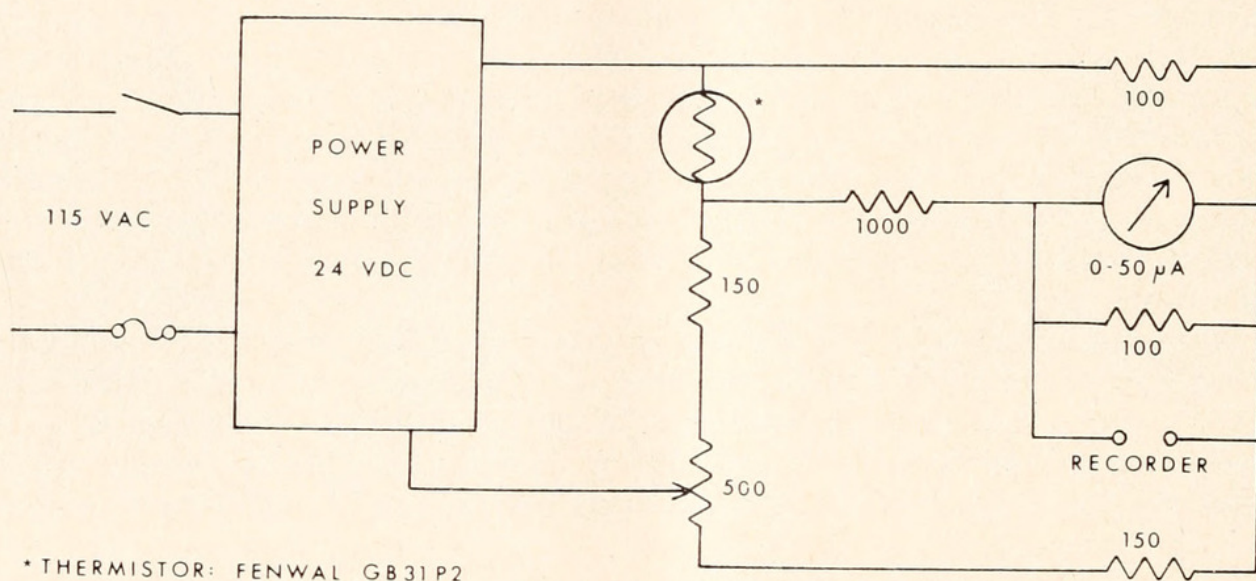


FIGURE 6. Circuit diagram of the thermistor flow-meter used for measurements in liquids at low speeds.

Finally, the probe could not be used in confined spaces (such as a spongocoel or oscular channel) at speeds below one cm/sec without inaccuracy resulting from local heating of the medium. The flow-meter was, however, not appreciably directional in its response; and its response time of about one second was amply short for present purposes.

For measurements on fresh material, the flow-meter was calibrated with the probe in a motor-driven revolving cylindrical bowl of sea water, 20 cm in diameter and 10 cm deep. In practice, the bowl was rotated until the water inside was moving at the same angular rate as the bowl itself; then the probe was lowered into the water near the center and slowly moved radially outward while the output of the meter was recorded. If the probe remained in one position for more than a few seconds, local heating and/or retardation of the medium gave a spurious reduction in the output of the meter.

For measurements on models in fresh water, the flow-meter was calibrated in the linear flow tank simply by measuring with a stop watch the time necessary for a dye-marker to travel 150 cm and comparing the result with the output of the meter.

RESULTS

Fresh material

Most of the actively pumping sponges gradually reduced their activity during the course of the measurements in the flow tank; therefore it was necessary to determine the pumping rate in still water after every few measurements of total flow. Data from animals whose rates declined were discarded on suspicions of moribundity. Figure 7 shows the combined active and passive flow for a sponge whose pumping rate in still water did not vary detectably over the course of

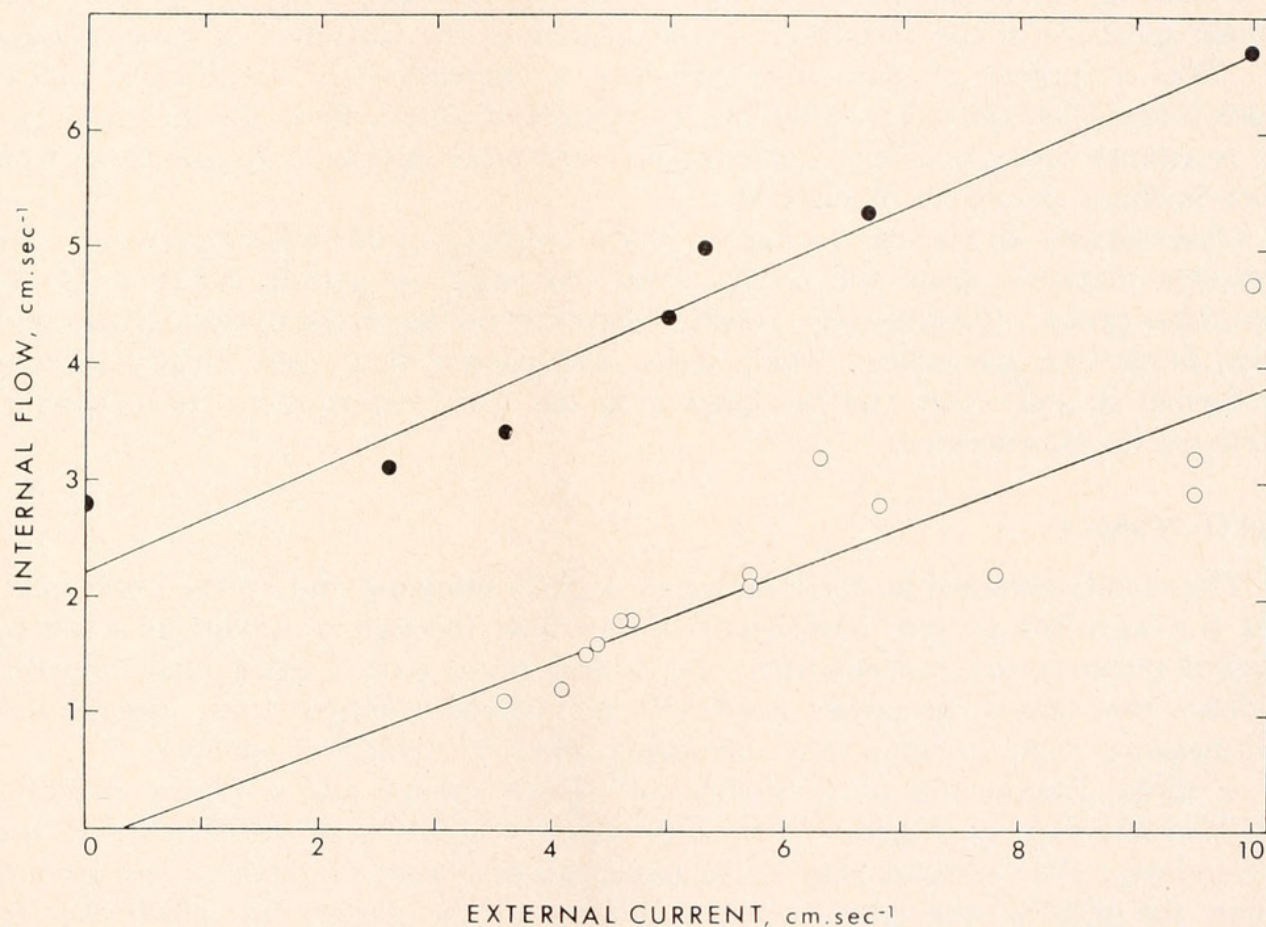


FIGURE 7. Flow across and through specimens of *Halichondria*. Closed circles—active pumping; open circles—specimens “turned off” by exposure to fresh water. The regression equation for the upper line is $Y = 0.450X + 2.207$; for the lower line it is $Y = 0.390X - 0.124$.

the measurements. It continued this rate of pumping for an hour afterwards, suggesting that the data for total flow through the sponge may be representative of flow rates in the normal habitat. Other specimens gave similar, but less regular and reproducible results.

Figure 7 also shows flow rates for sponges which, as determined by observations with dye markers, were not actively pumping. Although always less than the total flow through active sponges, these rates were substantial: at an external current of 7 cm/sec, the passive component was typically about one-half the total flow through an actively pumping sponge.

Neither the x nor y intercepts of the line fitted to the data on passive flow differ significantly from zero: at least in this range of speeds there is no evidence

of either residual pumping or of a non-linear relationship between internal and external flows. Moreover, the slopes of the lines for total flow and for passive flow through the sponges do not differ significantly: the active component appears to be simply "added on" to the passive flow and its magnitude does not depend on the strength of the external current in this range of speeds.

For the sponges for which data are presented here, mean internal oscular diameter was 4.9 mm (S.D. = 1.5, $n = 7$). The individual fingers were 31.0 mm (S.D. = 4.7) high and 12.1 mm (S.D. = 3.5) in outside diameter half-way between base and tip.

A plot of external current *versus* passive flow through a sponge gives a convenient measure of the resistance of the animal to the induction of flow through it. The reciprocal of the slope provides a dimensionless "resistance index" which lumps all of the factors affecting the efficacy of passive flow; for these sponges, the resistance index is 2.56. Comparisons with other species and specimens from other habitats should be of interest.

Observations on the encrusting or "hard" variety of *Halichondria* were made with dye markers, since the oscula were too small to permit insertion of the thermistor probe. Qualitatively, results differed in no way from those obtained with erect, finger-like specimens. Both active and passive flow were clearly evident, the former in still water and the latter after the usual exposure to fresh water to inactivate the choanocytes.

Model sponges

The results obtained on fresh material, actively pumping and "turned off" imply that the so-called passive component of the flow through a sponge is a purely physical phenomenon, independent of movement of any part of the animal. Further evidence that active processes need not be invoked emerges from observations and measurements on completely non-living, physical models of sponges.

A visual comparison of a "turned off" fresh sponge and a plastic model is provided by Figures 2 and 3. In both cases, a solution of Rhodamine B was injected near the upstream side of the basal end of sponge or model a few seconds before the picture was taken. The similarity of the pattern in which the dye solution emerges from the oscula is clearly evident.

A quantitative view of the flow induced in a model is provided by Figure 8. This model (Fig. 4) incorporates analogs of incurrent and excurrent canals as well as flagellated chambers, although it is still a very crude imitation of the array of channels in even a simple sponge. In particular, it proves impractical to reproduce the minute dimensions and enormous numbers of internal channels of a sponge, and it is convenient to construct a model somewhat larger than the size of the *Halichondria* fingers. This model is about twice the height of a real finger, and thus an equivalent flow is achieved when the external current passing the model is half that passing a real sponge.

The behavior of model and real (turned off) sponges are, nevertheless, quite similar; even the resistance indices (2.30 and 2.56) do not differ much if the data obtained on the model with external currents below 11 cm/sec are considered. It appears that the larger size of the channels in the model roughly compensates for their fewer numbers.

The principal difference is the lower slope of the curve for the model obtained at external currents above 11 cm/sec. Limitations of the sea-water flow tank precluded making equivalent measurements on fresh sponges, particularly since the appropriate velocities would have had to be above, not 11, but 22 cm/sec. However, the reduced slope is most likely to be an artifact of this particular model. When a very loosely-fitting and porous collar shielded the cylindrical portion of the model from an external current above 11 cm/sec, the flow through the model increased. At lower external currents, the collar was without effect. Perhaps

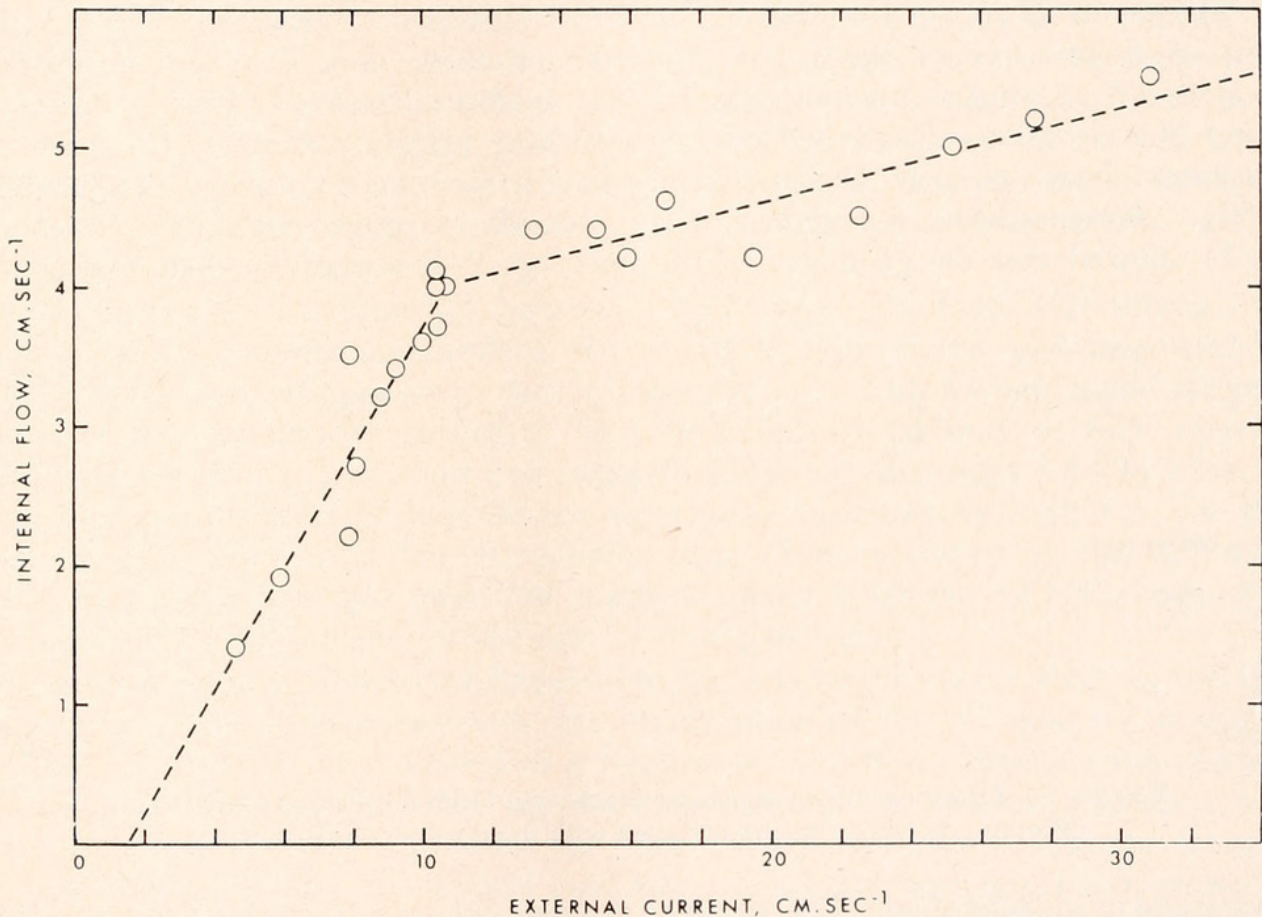


FIGURE 8. Flow across and through the model shown in Figure 4. Below an external current of 11 cm/sec the regression equation is $Y = 0.436X - 0.647$; above 11 cm/sec it is $Y = 0.066X + 3.29$. Flow was undetectable (less than one cm/sec) through the model when the "ostia" were blocked.

the unrealistically large diameters of the "ostia" in the model permitted significant entrainment at the higher speeds, thus opposing the entrainment at the osculum.

In addition to the model sponges shown in Figure 3 and 4, several others were constructed and tested with dye markers for passive flow, the latter by members of the Experimental Invertebrate Zoology Course (1972) at the Marine Biological Laboratory. Ms. Sarah E. Swank made a conical, crater-like model, 3 cm high, with a ring of large collecting channels directed upward and entering the common spongocoel just below the osculum. Mr. Duen Yen devised a vase-like model, 12 cm high, consisting of a wire framework wrapped with percale cloth, and producing more numerous and tinier pores than could be made of metal. Both of

these models permitted substantial induction of internal flow by movement of the medium. Indeed, our impression, based on a total of six "sponge" and two "archeo-cyathid" (Balsam and Vogel, 1973) models, is that effective designs may vary greatly in their details. The basic constraints of the scheme are little more than small input pores and a large output opening, the latter, at least, exposed to a transverse current. It may prove to be the case that sponges of a wide variety of shapes and sizes eventually show evidence of significant passive flow.

Model oscula

The oscula of sponges are not limited to sharp-edged, chimney-like holes at the ends of fingers, as in these *Halichondria*. Rather, they display considerable diversity, from rimless openings on the flat surfaces of some sponges, to small, crater-like elevations distributed over a branching array of cylinders, or holes on the inner surface of large, basket-shaped sponges (see, for example, DeLaubenfels, 1950). Measurements on models of the mounds of prairie-dogs (Vogel, *et al.*, 1973) showed that the geometry of the openings is important in determining the

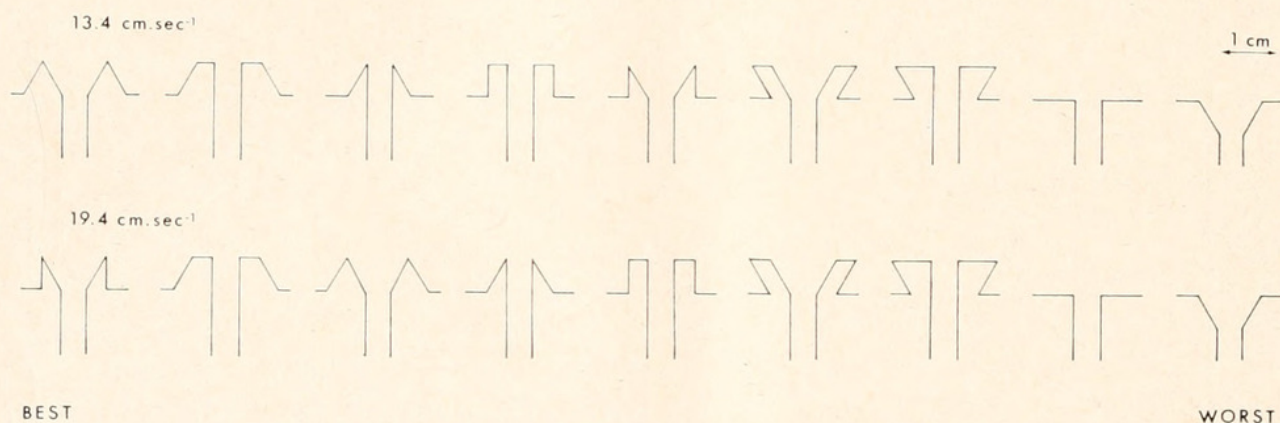


FIGURE 9. Ordering of test apertures from most to least effective exits at two different currents; results obtained with the apparatus of Figure 5.

magnitude of induced flow. The shape of the exit hole is of particular consequence, apparently in connection with the phenomenon of viscous entrainment.

Nine apertures were arranged from best to worst exits by testing one against another in enough combinations to produce an unambiguous ordering. Figure 5 shows the apparatus used for these comparisons. The results, given in Figure 9, prove rather complex. In general, sharp-edged openings are better exits than are blunt openings, and apertures which protrude from the surface are better than openings flush with the surface; this is essentially the same picture which emerged from the investigation of prairie-dog mounds. But the details of choices among internal tapers, external tapers, or combinations of the two prove dependent on, at least, the velocity of the external current. The dependence on velocity certainly indicates a relationship with the Reynolds number (size of object times density of a medium times velocity divided by viscosity). Thus it appears that a wide variety of shapes may be effective in inducing flow through a sponge, and that the optimum exit for a particular circumstance should depend in a complex manner on the overall shape and size of the sponge and on the currents in its habitat.

DISCUSSION

A simple maneuver, immersion in fresh water, permitted observations of induced flow in the absence of choanocytic pumping. But all sponges, as far as is known, do have choanocytes; and, it appears, they pump water with only occasional periods of quiescence (Reiswig, 1971). How, then, are passive flow and the operation of the choanocytes interactive?

According to the present data, the induced, passive flow achieves a magnitude comparable to that of the active, pumped flow at very low rates of movement of the surrounding medium. The induced rate matches the active pumping rate of about 2.5 cm/sec when the medium is moving at slightly under 6 cm/sec; above this value, the passive component of flow through the sponge exceeds the active rate. The active rates reported by others are somewhat greater than that found here: Parker (1914), Bidder (1923), and Reiswig (1971) mention rates most of which are between 5 and 15 cm/sec. Still, the rate at which fluid passes the choanocytes, even when they are fully active, should be strongly dependent on the rate of movement of the medium.

Furthermore, the difference between passive flow and total flow through the sponge is substantially independent of the rate of flow of the medium; in short, the active component appears to remain constant. No evidence was found suggesting that the choanocytes reduce or stop their flagellar activity at high rates of flow of the medium, and none was expected following Reiswig's (1971) observation that the quiescent periods do not correspond to unusually high (or, for that matter, low) currents in the surrounding sea. The constancy of this difference between passive flow and total flow suggests that the efficacy of the choanocytes as pumps is not dependent on the rate of flow past them.

By analogy with simple mechanical pumps, one might expect that, as the flow rate through the sponge increases, the contribution of the choanocytes would be reduced in absolute value as well as a fraction of total flow. Finding the opposite result raises the suspicion that the flagella operate in a manner analogous to a variable pitch propeller: perhaps the rate at which waves propagate along a flagellum is a function of the local flow rate. Similarly, one might expect that it would be energetically advantageous for a sponge to deactivate its flagella at high rates of passive flow. But, of course, sponges are preeminently filterers, and perhaps the filtering function of the choanocytes requires continued flagellar action.

As mentioned earlier, passive flow in sponges can result from the operation of several physical mechanisms, either singly or in combination. While the present data do not permit us to distinguish the particular contribution of each mechanism, Bidder's (1923) elaborate measurements on a specimen of *Leuconia* (referred to in the paper as *Leucandra*) permit some suggestive calculations. Application of Poiseuille's law,

$$Q = \frac{\pi \Delta P a^4}{8 \mu l} \quad (1)$$

(where Q is total flow, a is the radius and l the length of a pipe, and μ is the viscosity of the medium) to his data yields a pressure drop of 67.2 dynes/cm² for his observed flow rate of 8.5 cm/sec at the osculum in otherwise still water. The

first and third mechanisms for passive flow described in the Introduction depend on the operation of Bernoulli's principle. According to the latter

$$\Delta P = \frac{1}{2}\rho V^2 \quad (2)$$

(where ρ is the density and V the velocity of the free stream). If we assume that one opening or set of openings (here, the ostia) are at stagnation points or otherwise still water of the same total head of pressure as the free stream and further assume that the other opening (here, the osculum) is normal and exposed to the free stream, then a velocity of 11.6 cm/sec across the osculum would produce the requisite pressure drop of 67.2 dynes/cm².

Bidder's *Leuconia* and the present *Halichondria* are not dissimilar in structure; the former are merely somewhat longer (10 cm) and narrower (0.8 cm) than the latter (3.1 × 1.2 cm). Moreover the velocities (8.5 cm/sec through the sponge and 11.6 cm/sec across it) are not substantially different from the present results. Thus the assumptions that pressure is generated according to Bernoulli's principle and resisted according to Poiseuille's law might account for the magnitude of the passive flow observed.

But these assumptions do not explain the influence of oscular geometry on passive flow; the latter seems more in accord with an important role for viscous entrainment (the second mechanism in the Introduction). Moreover, if the expression for pressure drop (2) is substituted for the pressure in (1), it becomes clear that flow through the sponge should be proportional to the square of the velocity of the medium. In fact, the relationship (Fig. 7) proved closer to the first than to the second power. A mechanism based on the viscosity of the fluid, such as entrainment, could account for the greater than expected efficacy of passive flow at low speeds. Still, the exact dependence of passive upon external flow is not decisive, since any flow through the sponge will relieve the pressure drop calculated by Bernoulli's equation, greatly complicating the analysis.

If flow can be induced in a sponge with the modest external currents used here, the more rapidly moving water of most sponge-occupied habitats (see DeLaubenfels, 1954) should cause substantial flow. Yet the phenomenon of passive flow has hitherto escaped attention. Has any previous investigator made observations which should have disclosed a passive component of flow through sponges? Perusal of the relevant literature has turned up no case in which appropriate observations failed to detect passive flow. The usual difficulty seems to have been that work on flow through sponges has been done in a laboratory in otherwise still water.

Reiswig (1971), however, carried out extensive field study of the pumping activity of tropical Demospongiae; this latter work thus merits close attention. Both short and long term records of pumping were made, with continuous recording of oscular velocities for up to six days and sequential measurements on some specimens for up to three month periods. Unfortunately, his current recorder had a response time of about 30 seconds, so changes in flow through a sponge as individual waves passed were not detectable. Also, he reports no measurements of ambient currents. Reiswig does report that, for his main shallow-water species, "maximum pumping activity occurs when water circulation over the habitat is maximal."

Furthermore he mentions that thick-walled sponges with high pumping velocities are common in high turbulence areas on the outer reefs, while low-velocity, thin-walled forms predominate in low-turbulence regions. If turbulence is equated with ambient current strength, this distributional pattern could constitute evidence of adaptation to the use of passive flow: where the water moves more rapidly across a sponge it could induce flow through a greater thickness of wall.

To make use of induced flow, a sponge must have its osculum exposed to moving water. To penetrate the boundary layer of semi-stagnant water and expose its osculum, a sponge will have to protrude further from its surface of attachment if the ambient movement is slight than if the current is swift. It is therefore significant that from Grant (1825) onward, observers have noted the expected relationship (both inter- and intraspecifically) between the shapes of sponges and the characteristics of their habitats. For example, concerning *Halichondria panicea*, DeLaubenfels (1949, page 17) states, "Oscules conspicuous, 1-4 mm in diameter. The tissues of the sponge are elevated around these vents, so that they resemble craters of tall volcanoes. There is a rough correlation between the speed of currents at the sponge's location and the height of these volcanoes. Where the surf dashes back and forth, *panicea* is nearly smooth, but where it grows in comparative calm, the oscular chimneys may be elevated two or even five cm. In the latter case the width at the base of the tower is about 1 cm." The same author (1947, page 39) comments more generally, "Currents certainly modify sponge shape. One may notice where rocks are pounded by surf, that the sponges are regularly of the encrusting habitus. Elsewhere some of the same species may have the same shape, and give indication that such is the inherent tendency of the species, but many kinds of sponges, when in calmer waters, reveal their inherent tendency to proliferate and to have a ramose or otherwise erect shape." Such statements, although not definitive, clearly suggest that passive flow is of some importance in nature.

The principal direct evidence of passive flow in the normal habitat of sponges is the qualitative observations of M. C. LaBarbera and D. I. Rubenstein, Duke University, Department of Zoology (personal communication) in the Florida Keys. They watched a solution of methylene blue be taken up from around basket and columnar sponges with terminal oscula alternately exposed to strong surges and relatively calm water in a six to ten second cycle. The flow rate through the sponges was markedly dependent on the ambient current, being very low during the calms and high during the surges. They also noted that any columnar sponge with several vertical columns was invariably oriented with the columns in a row perpendicular to the direction of the surge; the latter arrangement should maximize exposure to moving water.

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SUMMARY

1. If a sponge is exposed to moving water, it is physically possible for water to pass unidirectionally through it without active pumping by the choanocytes; mechanisms presented for such "passive flow" predict flow from ostia to oscula.
2. In actively pumping *Halichondria*, water passes more rapidly from ostia to oscula in the presence of ambient currents; water flows through freshly killed *Halichondria* only when the surrounding medium is in motion.
3. Quantitatively similar passive flow may be induced by motion of the medium in a variety of physical models of sponges.
4. The efficacy of the induction of passive flow depends in a complex manner on oscular geometry although, in general, sharp-edged, protruding apertures are the most effective exits.
5. These apparently novel results are consistent with much earlier literature on the structure, behavior, and ecology of sponges.

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