

## Current-induced flow through living sponges in nature

(hydrodynamics/fluid mechanics/Porifera)

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**ABSTRACT** Flow velocities through and immediately adjacent to the excurrent openings (oscula) were measured in eight species of marine sponges in their natural environments with a two-channel thermistor flowmeter. Flow through the oscula was positively correlated with both normal and artificially augmented ambient flow in both normally pumping and inactive animals. These results indicate that the passage of water through these sponges is, in part, induced by ambient currents.

As a consequence of any of several physical mechanisms, internal flow through a structure may be induced by the flow of an external medium across that structure. Consider, for example, a fixed tube open at both ends exposed to a moving fluid. Flow through the tube may be driven by the increased pressure at an upstream-facing opening, by the reduced pressure at an elevated aperture with its axis normal to the external current (both according to Bernoulli's equation), and by the reduced pressure due to viscous entrainment at any opening normal to the external current. (1, 2).

Organisms may take advantage of this phenomenon to induce flows through themselves or their domiciles. Of the various groups of organisms that might do so, the sponges constitute the most inclusive taxonomic category. Most of the members of the entire phylum seem morphologically and ecologically appropriate: these sedentary animals commonly filter-feed in moving water, with fluid entering tiny pores in their walls and leaving through much larger openings usually well-removed from the substratum. Flagellated cells within the sponges are demonstrably capable of driving substantial filtration currents; the present question concerns the existence of flow induced by the external medium and its magnitude relative to actively pumped flow.

The suggestion that some of the flow through sponges might be a passive consequence of ambient currents was based on observations on physical models (1), and current-induced flow could also be demonstrated on living sponges in a laboratory flow tank (3). However, steady flow in a tank, while permitting straightforward comparisons with models, is far from the situation encountered by a sponge in nature; furthermore, the animals that actively pumped water in a tank did so at rates substantially lower than those expected in the field. The applicability of the laboratory observations to sponges in their natural environment has therefore been questioned (4).

I now report the results of recordings of the flow of seawater through and immediately adjacent to living sponges in their normal habitats. The pumping activities of the present animals range up to an order of magnitude above those previously examined in the laboratory. Nonetheless, the correlation between ambient current and flow through the sponges is still evident. Artificial increases in ambient flow are associated with increased flow through the animals, and inactivated sponges show the same purely passive internal flow as previously observed.

### MATERIALS AND METHODS

Measurements were made *in situ* on live sponges that occur within a few miles of the Bermuda Biological Station. Identification was based on DeLaubenfels (5). Together with the numbers of specimens of each, the species were the following: *Cliona lampa*, 1; *Haliclona variabilis*, 2; *Haliclona viridis*, 5; *Ircinia fasciculata*, 5; *Leucetta floridana*, 2; *Sphaciospongia othella*, 1; *Tedania ignis*, 4; and *Verongia fistularis*, 3. These species constitute an assemblage of considerable diversity. All are in the class Demospongia except *Leucetta*, a calcareous sponge. Each has erect, finger-like processes with apical oscula, except *Sphaciospongia* and *Tedania*, which are broader and rounder, and *Cliona*, a low, hard, boring form. *Verongia* and *Ircinia* have thicker (1.3–3 cm diameter) fingers with coarsely conulose surfaces; the *Haliclonas* and *Leucetta* have thinner (1–1.5 cm diameter) fingers with punctiform surfaces. *Tedania* and *Sphaciospongia* are smooth. Oscular diameters ranged from 0.5 to 1.0 cm, and the oscular rims were round and unbroken.

Measurements were made at four locations, two (Ferry Reach and Long Bird Bridge) subjected to tidal currents and the others (both in Harrington Sound) mainly to wave-induced local flow. Depths ranged from 1 to 2.5 m. The animals were located on the upper surfaces of rocks, on a vertical embankment, or on the sloping rock floor of shallow caves beneath the shore line. Continuous recordings of flow usually lasted less than 5 min, although a series of such recordings often extended up to an hour.

The omnidirectional, scalar flow detectors consisted of two self-heated bead thermistors, 1 mm in diameter; circuitry and performance of the entire two-channel flowmeter have been described elsewhere (6). In practice, the "inside" thermistor was positioned 5–10 mm beneath the oscular rim while the "outside" thermistor was about 4 cm lateral to the sponge and at about the same perpendicular distance from the substratum as the middle of the finger. The data are estimated to have an imprecision of no more than  $\pm 10\%$  at flows above  $1 \text{ cm sec}^{-1}$  and  $\pm 20\%$  from 0.5 to  $1 \text{ cm sec}^{-1}$ . The minimum detectable flow was  $0.2 \text{ cm sec}^{-1}$ .

At all sites, flow was cyclic, but rather irregularly so, with considerable variation in speed, direction, and period. The period between flow maxima ranged from about 1 sec for Harrington Sound to  $\frac{1}{4}$  sec at Long Bird Bridge, as observed visually with dye and from the recordings. The response time of the flowmeter, about 0.2 sec, thus was adequate for present purposes. Observations with dye indicated that the pattern of flow through an osculum, either pumped or induced, was not substantially affected by the presence of a thermistor probe. Under no circumstances were the sponges visibly deflected by the currents.

A more serious problem arises from the unavoidable physical

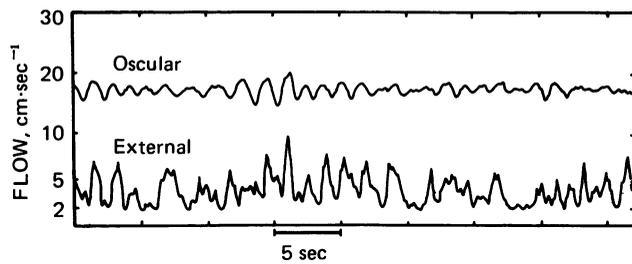


FIG. 1. Natural currents: flow through and adjacent to a *Verongia* in Harrington Sound. The originally logarithmic record from the flowmeter has been approximately linearized.

separation of the two probes and the irregular flow at these sites. Probes 4 cm apart typically record the same frequency of maxima and minima, but even in the absence of an animal they are exposed to somewhat different amplitudes and to major differences in the phase of these cycles. Thus, one probe may be exposed to a change in flow as much as a second before the other, and minor eddies may miss one probe entirely. For this reason, the points in Figs. 4 and 5 were generated by visual matching of simultaneous records, with a deviation of up to 0.5 sec permitted in matching maxima and minima. It should be noted that other schemes for correlating these records, including direct superposition, gave similar results, although with greater scatter of points.

Data cited here were obtained on calm days, so that wind-induced water movements were slight. It was not possible to perform the requisite underwater tasks on windy days due to excessive movement of both water and investigator. Instead, rapid localized water movements were produced by fanning sponges and probes with swim fins in a purposely irregular manner.

Sponges were inactivated by bathing them with fresh water as suggested by Parker (7) and previously found satisfactory (3); in practice, a small plastic bag of fresh water was held over a sponge finger for a few minutes.

## RESULTS AND DISCUSSION

When ambient flow is minimal, a steady current through the osculum presumably reflects the pumping activity of the

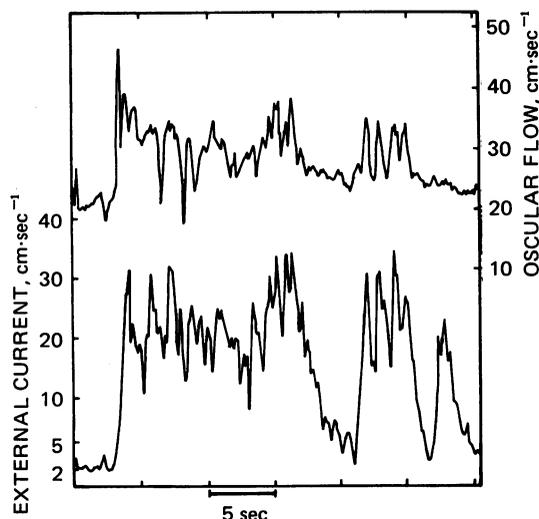


FIG. 2. Current augmented by fanning: flow through and adjacent to a *Verongia* in Harrington Sound living in a more sheltered location than that of Fig. 1. Fanning began after about 3 sec of recording. Left ordinate applies to lower records, right ordinate to upper. Records approximately linearized.

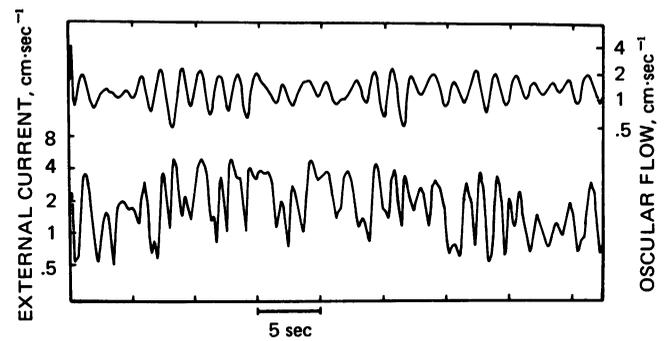


FIG. 3. Natural current, inactive sponge: flow through and adjacent to a *Haliciona viridis* in Harrington Sound after inactivation. Left ordinate applies to lower record, right ordinate to upper. Original logarithmic record.

sponge. For the present animals, such active pumping rates ranged from 7.5 to 22  $\text{cm sec}^{-1}$ . No particular correlation was noticed between this pumping rate and either species, size, or habitat. And these flow speeds are similar to those, between 7.9 and 17.3  $\text{cm sec}^{-1}$ , obtained by Reising (8) on three very much larger species. I estimate that the rate of water volume transport per unit volume of sponge per unit time resulting from active pumping is within a factor of two of 0.20  $\text{sec}^{-1}$  for the present animals. Again, the similarity with Reising's results, 0.085–0.27  $\text{sec}^{-1}$ , is notable: in the present animals each osculum drained about 20  $\text{cm}^3$  of sponge, whereas in his animals each osculum drained between 100 and 50,000  $\text{cm}^3$ .

Fig. 1 gives a typical pair of recordings from an undisturbed animal exposed to natural currents. At this location, currents were particularly irregular with respect to both speed and direction. Yet the superposition of variations in the external current on the oscular flow is clearly evident, even if the amplitude and phase of these variations are not precisely followed. It should be noted that external currents much lower in magnitude than the oscular flow still affect the latter. Indeed, only in a few of the most actively pumping sponges in the most sheltered locations could the variations in external current not be discerned in recordings of oscular flow.

In every case, artificially augmenting the ambient current by fanning the sponge increased the flow through the sponge

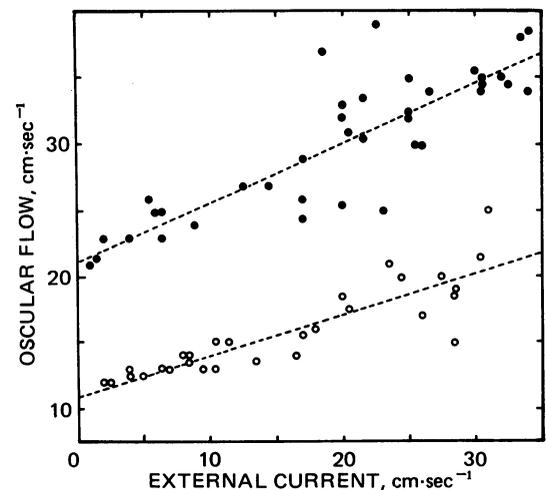


FIG. 4. Flow through and adjacent to the *Verongia* of Fig. 2 (●, upper line) and an *Ircinia* at Long Bird Bridge (○, lower line). For the *Verongia* the regression equation is  $Y = 0.44X + 21.3$  and the coefficient of determination ( $r^2$ ) is 0.73; for the *Ircinia* the equation is  $Y = 0.31X + 10.9$  and  $r^2 = 0.77$ .

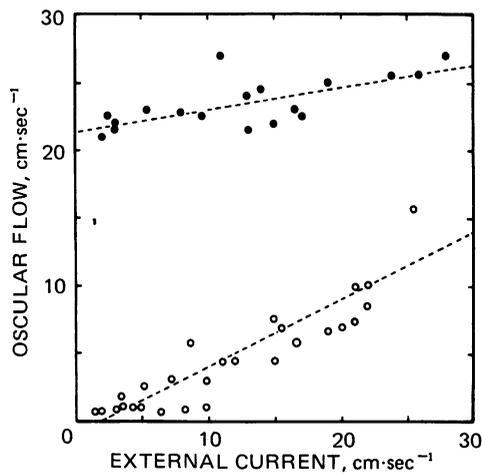


FIG. 5. Flow through and adjacent to the *H. viridis* of Fig. 3 before (upper line) and after (lower line) inactivation, in both natural and augmented currents. For the upper line the regression equation is  $Y = 0.16X + 21.4$  and the coefficient of determination ( $r^2$ ) is 0.49; for the lower line the equation is  $Y = 0.47X - 0.93$  and  $r^2 = 0.85$ .

and increased the extent to which flow inside tracked the external current. Fig. 2 presents paired records of such augmented currents. Even very rapid changes in external current were reflected in alterations of flow through the animals. By analogy with electrical devices, these sponges might be considered purely resistive and noncapacitative with respect to flow, at least within the temporal resolution of the flowmeter. Except as mentioned below, animals resumed their original oscular output rate after exposure to augmented currents.

Fig. 3 shows a recording from an inactivated sponge. Flow rates through inactivated animals were much below normal except at very high levels of ambient current, and the internal flow appeared to depend entirely on external current. The performance of artificially inactivated sponges could not be distinguished from that of animals that were initially inactive or that spontaneously stopped pumping.

The relationship between flow through and adjacent to a sponge emerges more clearly from plots of paired data of maxima and minima from the recordings. The slope of such graphs gives a measure of the magnitude of flow induction in the particular animal; the  $y$ -intercept indicates the active component of internal flow. Fig. 4 presents data from an *Ircinia* with a relatively low active pumping rate and from the *Vernonia* of Fig. 2, a particularly active animal. Fig. 5 is the same *Haliclona viridis* as in Fig. 3, before and after inactivation.

Several sponges were inactive when entered with a probe, with flow through the osculum occurring only in response to movement of the surrounding water. Several others rapidly

reduced their activity over a period of several minutes after penetration. All such cases involved either *Tedania ignis* or *Haliclona viridis*. It appears that accidentally pressing the oscular or body wall with a probe is often a sufficient stimulus to trigger cessation of pumping in these species.

These observations show that ambient currents can and do increase the rate at which water under natural conditions passes through sponges. The essential similarity of results obtained on the present eight species, the similarity of the present oscular flow rates with those obtained on much larger sponges, and the relative structural homogeneity of the phylum together suggest that the phenomenon of flow induction is likely to be widespread among sponges. The overall impact on the energy required for filtration by sponges is probably substantial, but a precise evaluation of the role of current-induced flow in the life of any particular sponge requires information as yet unavailable.

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