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Flow around phoronids: Consequnces of a neighbor to suspension feeders

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Flow around phoronids: Consequences of a neighbor to suspension feeders

Abstract—Dye visualization was used to assess the effects of closely spaced conspecifics to the flow microhabitat of the benthic suspension feeder *Phoronopsis viridis* Hilton (Phoronida), which lives in dense populations over a wide range of natural densities. Spacing between upstream-downstream neighbors affected water movement near the animals and the source of water processed by their filter-feeding tentacles. Visualization of flow around and between pairs consisting of living and model *P. viridis* revealed that water encountered tentacle crowns (lophophores) via upward transport from near the sandy substratum rather than from above the lophophore, close spacing of individuals (< 1 lophophore diam) inhibited this upward flow for the upstream neighbor, and turbulence generated by an upstream neighbor increased the useful area of feeding surface of the lophophore in the downstream individual. Upward movement of water is important because benthic food particles are an important component of the diet of *P. viridis*. Thus the presence of neighbors within populations of *P. viridis* could enhance the incorporation of benthic food particles into their diets. The consequences to feeding of having a neighbor should shift from positive at low densities (> 1 lophophore apart) to negative at high densities (≤ 1 lophophore apart).

The presence of neighbors drastically alters the flow-microhabitat experienced by individuals living in groups of suspension feeders. Although flow-microhabitat affects the feeding performance of suspension feeders (Okamura 1984, 1985; Patterson 1984; McFadden 1986; Hunter 1989) and although interspecific and intraspecific enhancement or depletion of food commonly occurs in dense groups of suspension feeders (Okamura 1986, 1988; Peterson et al. 1984), few studies (O'Neill 1978; Merz 1984; Chance and Craig 1986) have examined the consequences to flow of spacing between individual suspension feeders.

The present study examines how spacing between upstream-downstream neighbors affects water movement near *Phoronopsis viridis* and the source of water processed by its filter-feeding tentacles. *Phoronopsis viridis* is a wormlike, tubicolous, marine suspension feeder that lives in dense populations (up to 20,000 m^{-2}) on the intertidal sandflats of northern California. Its diet is rich in benthic food particles that are captured by a ciliated crown of tentacles (lophophore). When the tide is in, this lophophore projects about 1 cm above a sandy bottom into a velocity gradient.

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The specific question addressed here is how does the presence of an upstream or downstream neighbor influence paths of water movement around an individual *P. viridis*? The results of these experiments represent a first step in addressing the more general question: what are the hydrodynamic and ecological consequences of the spacing of benthic organisms to the flow they experience adjacent to a substratum?

Phoronopsis viridis was collected from the sandflat in the University of California's marine life refuge at Bodega Bay (~120 km north of San Francisco), at ~0.6 m above mean lower low water. Live phoronids were removed from the sandflat and kept intact within their sturdy, sand-encrusted tubes. Tubes of adult *P. viridis* are ~15 cm long. Phoronids that were used in experiments at the Friday Harbor Laboratories, University of Washington, were sent in plastic bags inside an ice chest and maintained in circulating seawater tables at ~15°C; they were used in experiments within 6 weeks of their arrival. Phoronids that were used in experiments on the Berkeley campus were kept in the laboratory in glass aquaria at a mean temperature of 15°C and used in experiments within 1 week of their removal from the sandflat.

Water movement was visualized around pairs of phoronids by planting living and model animals into a nonrecirculating seawater flume (described by Nowell et al. 1981) at the Friday Harbor Laboratory and into a 450-liter recirculating seawater flow tank similar in design to that of Vogel and LaBarbera (1978) in Berkeley. The body of the Berkeley flume was 250 cm long and 30 cm wide. The working section contained a 20- × 20-cm sand-filled box into which phoronids and models were planted. This box was located 100 cm downstream of the flow straighteners. The beds of both flow tanks were covered with sand that had been scraped from the surface of the sandflat. The depth of water in the flow tank was 11 cm for all experiments in both tanks. All experimental velocities were determined by timing particles moving at 4 cm above the bottom. Except where specified, all experiments were conducted at four mean velocities: 1, 3, 5, and 10 cm s^{-1}. These velocities fell within the range of those measured in the field at 4 cm above the substratum (Johnson 1988).

Velocity gradients were measured in the Berkeley flow tank by taking streak photographs of particles moving with the water (Kodak Tri-X film: $f = 2.8$; ½ s at 1 cm s^{-1}; ¼ s at 3 cm s^{-1}; ⅛ s at 5 cm s^{-1}; $\frac{1}{15}$ s at 10 cm s^{-1}; Johnson 1988). A thin plane of water was illuminated in each photograph. Moving particles appeared as streaks. The velocity profile was determined by measuring the length of streaks at several heights above the substratum. The velocity gradient remained constant over the length of the working area. The boudary shear velocity u_*—a number that characterizes the slope of the velocity gradient (described by Nowell et al. 1981; Jumars and Nowell 1984)—ranged between 0.1 cm s^{-1} at an ambient velocity of 1 cm s^{-1} and 1.1 cm s^{-1} at an ambient velocity of 10 cm s^{-1}. This range of u_* is characteristic of flow over a sandflat environment (Eckman 1983; Johnson 1988). Observations of dye movement in the tank revealed that flow was laminar at velocities up to 3 cm s^{-1} and developed turbulence at velocities >5 cm s^{-1}.

Paths of water movement were visualized around phoronids by releasing neutrally buoyant fluorescein dye (mixed in seawater) 1 cm upstream from the leading phoronid and photographing the result (Fig. 1). Fluorescein dye was released through a hypodermic needle, 20 cm long (1-mm i.d.) that had been bent at the tip to prevent entrainment of dye in the wake of the needle. A 1-cm distance marked on the needle was used to determine scale in all photographs. The position of the needle relative to the animal was adjusted by micromanipulator. The flow rate of dye was controlled by adjusting the pressure in a 50-ml syringe with a screw that had been attached to the plunger of the syringe. Dye was released into ambient currents at the height of the lophophore (position 1 in Fig. 2), within 1 mm below it (position 2), and adjacent to the substratum (position 3) upstream of each pair.

Model phoronids were designed and constructed to be hydrodynamically similar to living ones stiffly oriented in an upright pos-

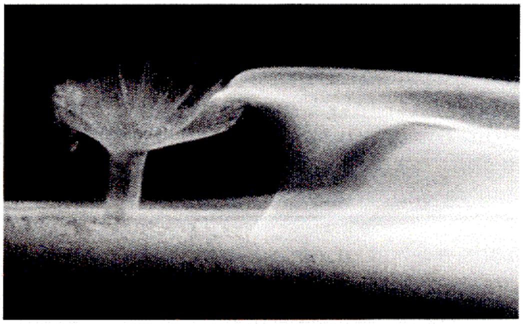

Fig. 1. Paths of water movement visualized around an isolated phoronid by releasing neutrally buoyant fluorescein dye (mixed in seawater) upstream and photographing the result. Height of animal is ~1 cm. Most water filtered by an isolated *Phoronopsis viridis* comes from below the lophophore and is captured on its downstream side (Johnson 1988).

ture. The construction, selection, and hydrodynamic characteristics of these models and the consequences of changes in posture to flow are described elsewhere (Johnson 1988). It was not necessary to consider the contribution of ciliary currents of living animals, as general water movement around *P. viridis* is a consequence of the interaction of its morphology with flow (Johnson 1988). It was not necessary to model the tubes of *P. viridis,* as only the bodies of living phoronids project above the surface of the sandflat (Fig. 3). The mean height of phoronids living in the flow tank, as measured from photographs, was 0.89 cm (7 animals, 116 observations, SE = 0.01), and phoronids planted into pairs maintained about the same height (Fig. 3). The height of the model phoronids above the bottom was set at 0.9 cm on the basis of these observations.

Water movement was observed and photographed around four types of pairs. Type 1 consisted of two live animals (one upstream, one downstream; Fig. 3). Water movement was observed around one type 1 pair. Type 2 consisted of a model upstream and a live animal downstream. Water movement was observed around one type 2 pair. Type 3 pairs consisted of a live animal upstream and a model downstream (Fig. 2). Water movement was observed around two type 3 pairs. Type 4 pairs consisted of two models (one upstream, one downstream). Water movement was observed around five type 4 pairs. All obser-

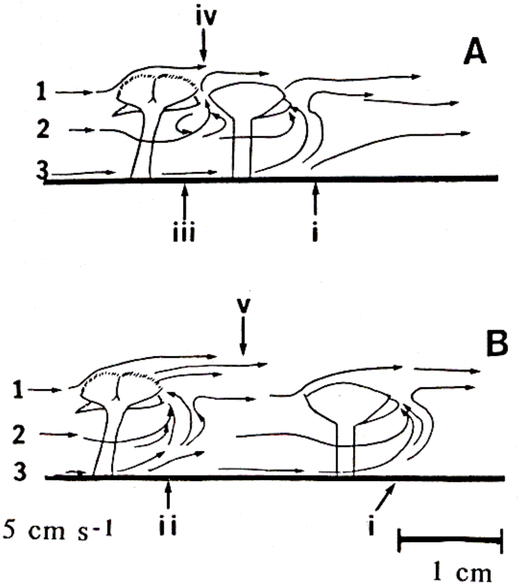

Fig. 2. Paths of dye movement, traced from photographs taken at a velocity of 5 cm $^{-1}$, around a living *Phoronopsis viridis* (upstream) and a model (downstream). Dye tracings represent the composite results from five photographs. Dye movement around pairs in which both members were live phoronids or both members were models was the same as shown here for a living and a model phoronid. Paths of dye movement observed around pairs spaced 0.6 cm apart (not shown) were the same as those shown here around pairs spaced 1 cm apart (A), and paths of dye movement around pairs spaced 1.5 cm apart (not shown) were the same as those shown here around pairs spaced 2 cm apart (B). Arrows represent paths of dye movement for dye that was introduced at the height of the lophophore (position 1), within 1 mm below the lophphore (position 2), and adjacent to the substratum (position 3) just upstream of each pair. Dye movement described in text.

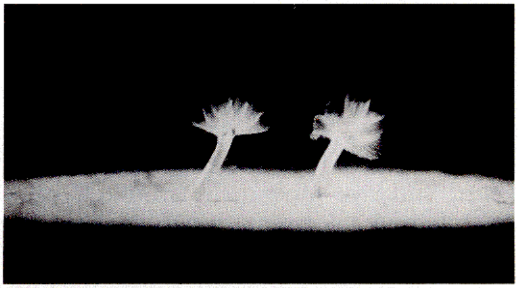

Fig. 3. Two live *Phoronopsis viridis* (one upstream, one downstream) spaced ~1.2 cm apart. Although they construct sturdy tubes, only the neck and lophophore of living phoronids project above the sand. Phoronids transplanted into the flow tank in pairs maintained about the same height.

vations were repeated several times at each velocity.

The resultant patterns of dye movement were photographed for one pair of each type. Type 1 was photographed in the Friday Harbor flume at 5 cm s^{-1}. Type 2 was photographed in the Friday Harbor flume at velocities up to 5 cm s^{-1}. Types 3 and 4 were photographed in the Berkeley flume at velocities up to 10 cm^{-1}.

Four spacings were used between the members of each type 3 and type 4 pair. Two of these spacings, 0.6 cm and 1.0 cm, were equivalent to the mean distance between nearest neighbors measured among phoronids living at low density (<0.60 phoronids cm^{-2}) and high density (>0.85 phoronids cm^{-2}) on the sandflats of Bodega Bay (Johnson 1986). The other two spacings, 1.5 cm and 2.0 cm, were equivalent to the extreme distances between nearest neighbors that were measured among phoronids living in these same high- and low-density areas. Type 2 pairs were observed at distances apart of 1.0 and 2.0 cm. Because of the difficulty of accurately spacing two live phoronids and having both of them cooperate simultaneously, experiments with two living phoronids were successful at only one spacing (1.2 cm) and one velocity (5 cm s^{-1}).

Flow around pairs of *P. viridis* shares some characteristics in common with flow observed around pairs of cylinders (Zdravkovich 1977). That is, repeatable patterns of water movement were observed that depended mostly on water velocity and on spacing between members of pairs. Dye movement around type 3 pairs (Fig. 2), consisting of a live *P. viridis* upstream and a model downstream, was the same as observed around all other types of pairs. Dye movement observed around type 3 pairs spaced 0.6 cm apart was the same as observed around type 3 pairs spaced 1 cm apart, and dye movement around type 3 pairs spaced 1.5 cm apart was the same as observed around type 3 pairs spaced 1 cm apart. Therefore, results are shown only for type 3 pairs spaced either 1 (Fig. 2A) or 2 cm apart (Fig. 2B). All subsequent lowercase Roman numerals in the text refer to Fig. 2.

Most water filtered by living phoronids entered the lophophore from an area below the crown of tentacles (i, ii, iv). This pattern is consistent with previous observations that most water filtered by isolated *P. viridis* came from below the lophophore and was captured on its downstream side (Fig. 1; Johnson 1988). The upward movement of water between adjacent lophophores could be accounted for in part by viscous entrainment, as relatively fast-moving fluid above the lophophores entrained more slowly moving water from between lophophores. Fluid shear that accounts for such viscous entrainment is a hydrodynamic consequence of slower water movement at the height of the lophophores (Fig. 4; Johnson 1988). Steep vertical gradients in velocity also create a vertical pressure gradient that results in upward movement of fluid (Vogel 1981; Eckman and Nowell 1984).

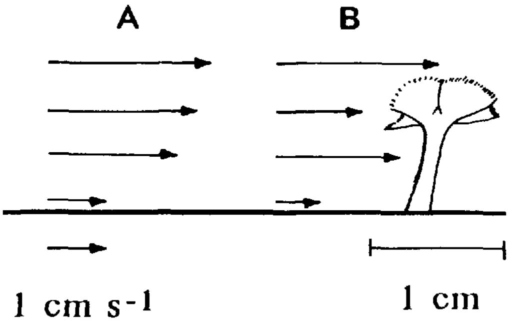

Fig. 4. The arrows in part A represent real velocities (data from Johnson 1988) just upstream of *Phoronopsis viridis*, as a function of height above the substratum. The arrows in part B represent velocities in the same horizontal plane as *P. viridis*, but are shown upstream for clarity. Velocity is slowed at the height of the lophophore. Interpretation given in text.

At velocities >1 cm s^{-1}, dye moved up off the substratum and into the lophophore on the downstream side of all downstream model phoronids in all pairs (i in Fig. 2), and all upstream phoronids that were >1 cm from their downstream neighbors (ii). Such paths of water movement should influence the flux of particles encountered by the lophophore. For example, although the influence of hydrodynamic factors on particle resuspension is complicated by biotic factors such as mucous binding of sediment by benthic diatoms and the density of other macrofauna (Luckenbach 1986), water moving up from the substratum should be enriched in benthic food particles such as the flocculent organics and benthic diatoms that form an important component of the diet of *P. viridis* (Ronan 1978). The degree of particle enrichment in this upward moving fluid should vary with the magnitude of the surface shear stress that results in particle erosion.

The relationship between surface shear stress and spacing between neighbors remains to be determined. Nowell and Church (1979), as well as Eckman et al. (1981), found that turbulence levels increased within arrays of roughness elements up to 12% cover (equivalent to natural low densities of *P. viridis*). At higher densities, there was a transition to skimming flow, which would result in decreased surface shear stress within arrays. However, patterns of surface shear stress in a population become much more complicated as the arrangement of neighbors deviates from even spacing (Johnson 1986, in prep.).

All downstream model phoronids, as a consequence of intercepting the turbulent wake generated by upstream *P. viridis*, captured dye-laden water around the entire lophophore. In contrast, isolated phoronids (Fig. 1; Johnson 1988) and the upstream member of pairs captured currents largely only on the donwstream sides of their lophophores (iv and v in Fig. 2). These observations suggest that, at spacings greater than approximately the diameter of one lophophore (> 1 cm), the presence of an upstream phoronid could facilitate feeding of a downstream phoronid by two mechanisms: moving water upward from near the substratum and creating a turbulent upstream wake that increases the area of lophophore used to capture currents by the downstream phoronid. Although upstream neighbors could also deplete water of food particles, it is unlikely that downstream individuals would filter much depleted water as the major excurrent flow of *P. viridis* is directed strongly upward (Johnson 1988). Any benefit to feeding would be shared by both members of pairs living in flow that changes direction with the tide.

At velocities <10 cm s^{-1}, upstream members of pairs spaced within one lophophore's diameter (~ 1 cm) of each other often failed to capture water moving off the substratum (iii in Fig. 2). In addition, water that recirculated below adjacent lophophores, as seen between lophophores of pairs that were within 1 cm of each other (iv), would be expected to be relatively depleted by the feeding activities of living phoronids. This region of recirculation was never observed between pairs that were spaced >1.5 cm apart (v). These observations generate the prediction that at high densities, where phoronids are generally within one lophophore distance of each other, there should a feeding disadvantage. Any feeding disadvantage would be shared by both members of pairs living in tidally dominated flow.

These results demonstrate that it is necessary to know the distance between neighboring suspension feeders before determining whether there are negative or positive consequences from neighbors. On the basis of observations of dye movement, at low density *P. viridis* would be expected to feed better in the presence of a neighbor than in isolation. At densities where individuals are too closely spaced (less than the diameter of one lophophore), however, feeding would be expected to be reduced. These predictions are supported by field studies. Sampling of the natural population of phoronids at Bodega Bay revealed that there was a negative association between adult body size and population density, and transplant experiments revealed that adults transplanted into natural low-density arrangements attained a larger size than those transplanted into natural high-density arrangements (Johnson 1986).

Although the specific effect of spacing on flow will differ as a consequence of morphology and flow regime (Jumars and Nowell 1984), density-dependent consequences to flow of spacing between conspecifics are certain to be important to suspension feeders other than *P. viridis*. For example, similar patterns of water movement to those observed in this study have been observed between simuliid fly larvae (Chance and Craig 1986) and around tubes of the polychaete *Lanice conchilega* (Carey 1983). These results support the hypothesis that spacing within groups composed of genetically identical feeding units will be subject to strong selection.

It would be expected that the consequences to flow of the uniformity in spacing often observed between feeding units of clones or colonies should facilitate feeding within such groups (Winston 1979; McFadden 1986). Further, in groups composed of individuals that can change position relative to each other, there should be flow-induced changes in position relative to neighbors. Such changes have been observed for sand dollars (O'Neill 1978), polychaete worms (Merz 1984), and simuliid fly larvae (Hart 1986). A feeding advantage has not been demonstrated for sand dollars or polychaetes. Merz (1984), however, found that water was depleted of particles as it moved through clusters of the polychaete *Eudistylia vancouveri* and hypothesized that there was potential competition for food in such clusters. Conversely, Hart (1986) found that simuliid larvae increased rates of particle ingestion when they dislodged neighbors that were within one body length upstream of them. Thus, the presence of suspension-feeding neighbors may sometimes facilitate feeding, but there are often negative consequences from close proximity.

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Evidence against incorporation of exogenous thymidine by sulfate-reducing bacteria

Abstract —The uptake of exogenous [^{3}H]thymidine by SO$_4^{2-}$-reducing bacteria (SRB) was tested in both pure culture and in marine sediments. Ten cultures isolated from mesohaline sediments of Chesapeake Bay, plus ATCC strain *Desulfovibrio desulfuricans aestuarii,* were incubated in SO$_4^{2-}$-reducing media with [^{3}H]TdR concentrations ranging from 2 to 100 nM. In most cases [^{3}H]TdR uptake levels were no more than a few times higher than Formalin-killed controls; SRB cells took up a maximum of 1.7×10^{-22} moles TdR cell^{-1} h^{-1}. Across all incubations, an average of 3.3×10^{23} SRB cells were produced (mol [^{3}H]TdR)$^{-1}$ taken up, compared to an average value of $\sim 2 \times 10^{18}$ cells (mol [^{3}H]TdR)$^{-1}$ in natural, oxic waters. In anoxic sediments the addition of molybdate, an inhibitor of SO$_4^{2-}$ reduction, significantly reduced amino acid metabolism but did not decrease [^{3}H]TdR incorporation into TCA-insoluble material. These data suggest that the thymidine uptake method may drastically underestimate bacterial production in samples where SO$_4^{2-}$ reduction is quantitatively important, such as nonsurficial marine and estuarine sediments and anoxic saline waters.

Measurement of the incorporation of exogenous tritiated thymidine into DNA by aquatic bacterial communities is becoming a standard technique for estimating bacterial productivity. Implicit to use of the TdR incorporation method is the assumption that all of the metabolically active bacteria in the ecosystem of interest are assimilating exogenous TdR into DNA. This assumption has proven valid for several aquatic systems, particularly oxic seawater (Fuhrman and Azam 1982; Moriarty 1986). Measurements of TdR incorporation by cells in the anoxic hypolimnion of a freshwater lake (McDonough et al. 1986) and in muddy sediments (Fallon et al. 1983) suggest, however, that anaerobic bacteria take up less exogenous TdR per mole of DNA produced than do aerobes, and that a smaller percentage of TdR taken up is incorporated into DNA.

During a study of the spatial and temporal distribution of bacterial activity in surficial Boston Harbor sediments, in which [^{3}H]TdR uptake was used as a measure of bacterial activity, we encountered several sediment sites that were anoxic and sulfitic to within millimeters of the sediment surface. A suggestion by Moriarty (1984) that SO$_4^{2-}$-reducing bacteria (SRB)—dominant bacteria in this type sediment—do not seem to take up exogenous thymidine prompted us to test that hypothesis. SO$_4^{2-}$ reduction can account for the majority of C flux from shallow-water marine sediments (Martens and Klump 1984) so that measurement of the productivity of these microorganisms must be included in any estimate of microbial production in such environments. Moriarty (1984) suggested that anaerobes with strict nutrient requirements may lack transport systems for TdR, citing in particular a personal communication from G. W. Skyring

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