

SUSPENSION FEEDING

The dynamic viscosity (μ) of corn syrup is about 24 Pa s, compared with 1.09×10^{-3} for seawater. The densities (ρ), in turn, are about 1360 and 1025 kg m⁻³, respectively. So consider the problem of catching a particle in seawater with a spoon of 2.5 cm width. I choose a spoon because you have some familiarity with its operation. Let's say that you operate the spoon at a speed, u , of 1 cm s⁻¹. A copepod nauplius may operate a feeding appendage at $u = 1$ mm s⁻¹. What length scale of naupliar appendage will the spoon or fork represent (both at 20°C)? Set up Reynolds-number equivalence as

$$Re = \frac{\text{Seawater}}{1.09 \times 10^{-3}} = \frac{\text{Corn Syrup}}{24}$$

$$Re = \frac{1030 \times 1 \times 10^{-3} \times L}{1.09 \times 10^{-3}} = \frac{1360 \times 1 \times 10^{-2} \times 0.025}{24}$$

Solving for L gives 1.5×10^{-5} m, or about 15 μ m. Now use a fork as what you might think would be a better capture appendage. You will find that it isn't of much use unless you trap the particle against the side of the container. This exercise is meant to drive home the difficulty of capturing particles at low Re. You now have experienced the principal difficulty of capturing a bacterium.

Put several specimens of the holothuroid *Cucumaria frondosa* or of another suspension feeder in the flume. Bigger is not necessarily better when it comes to choosing specimens. Put them in either sequentially so only one at a time is in the flume or space them far enough apart that flow around one animal is unaffected by flow around its neighbors. Observe the specimens at no fewer than two different flow velocities. When you are satisfied that you are observing typical behaviors (rather than oddities of a single specimen), answer the following questions or requests. You can incorporate your answers into the usual essay format (with diagrams and equations welcomed as usual) and take the questions in any order that you find convenient and compact, but check to make sure that you have answered each of them completely. Exercise ideas and terms from lectures and readings.

- (1) For each flow velocity, describe the characteristic flow pattern in the vicinity of the animal and in the vicinity of its feeding structures. Be sure to specify the orientation of the animal in the flow and the location of its tentacles or other encounter structures in the boundary layer. Don't forget what you learned about the three-dimensional features of flows around real objects in boundary layers.
- (2) Choose at least three different Reynolds numbers that would be useful in understanding suspension feeding by this species (and by most other suspension feeders). More than one may be the same type of Re , e.g., two body Re with different velocity and length scales. Specify why each would be useful and make clear what length and velocity scales would need to be measured to calculate a numerical value for each Re . By putting dye in the right places, decide whether the flow regime described by each Re (at each of your two flume settings, so you need six separate answers) is laminar, transitional or turbulent. Remember that laminar flows follow contours of objects or of the seabed, transitional ones show some flow separation, with attached or shedding eddies, and turbulent flows show a more chaotic pattern.
- (3) Make a case for whether the postures and orientations that you observe are passive (induced by the flow), active or some combination of the two.
- (4) Where does encounter with food particles happen? Be as specific as you can (e.g., on the side-stream face of the "trunk" of the dendritic tentacles). How are they retained?
- (5) How do the flows characterized by your three or more Re combine to influence encounter rate

with suspended particles and retention efficiency of them? Again, consider both flow-velocity regimes that you create. You may want to import (pipette in) some crud from another tank to make seston to help answer this question. Hint: This animal, like most passive suspension feeders on the seabed, encounters mostly by direct interception, with a little help from inertial impaction in the case of large, organic aggregates. So, look for stagnation points, *i.e.*, places on the body where oncoming flow streamlines diverge when they encounter the object — actually the point or line where flow velocity is zero. That hint is not as helpful as it would first appear, because if the flow is not laminar stagnation points can be on the downstream side of the body (with respect to the general direction of flow in the flume channel) and time varying.

A CAUTIONARY REMINDER

You may choose to use a body Re for the whole body or for any body part that projects into the flow. Recall that body Re numbers of the garden variety are defined by a single velocity scale, which means that the oncoming flow is uniform in velocity. Channel, pipe and roughness Re don't have this same limitation. The simple warning is that if flow is turbulent upstream of the body of interest in your Re , you can't expect the "imported" turbulence to vanish immediately, although a dense array of structures may fairly rapidly decrease average velocity through the array in ways that we will revisit. Turbulence, whether locally generated or imported from upstream, will affect the operation of a suspension-feeding appendage.

EXERCISE YOUR BRAIN, THINK ABOUT RATES, EFFICIENCIES AND TRADE-OFFS

Think about the hypothetical problem of maximizing ingestion rates. We'll worry later about the real maximization problem that all heterotrophs have, *i.e.*, of maximizing the net rate of absorption. These maximization problems need realistic constraints (*e.g.*, a finite size of mouth or volume of gut), and accurate mathematical models of the process may involve the risk of getting eaten if you come out to eat.

Cucumaria does not do a whole lot of food rejection, so how does ingestion rate, I , reflect encounter rate, E . The answer is EZ . That is, $I = EZ$. So what is Z , and what are its dimensions? For now, let's keep it simple and consider I (*not me*) to have dimensions of numbers (of particles) per unit of time [$N T^{-1}$]. Ingestion rate should be in the same dimensions (unless you can think of better ones). Now, what must be the dimensions of Z ? Right, it is a trick question, as Z must be dimensionless. So Z is the retention efficiency.

The tentacles are dendritic, which is a common geometry in exchange structures. Your job, should you decide to accept it, is to design a dendritic collector to maximize the rate of ingestion. Make sure that you watch how *Cucumaria* keeps its retention efficiency high and roughly constant. The tentacles are unloaded before they become so loaded that retention efficiency would suffer much. So, since *Cucumaria* has solved the design problem of retention ($Z \approx \text{constant}$) your job is to maximize encounter rate. From playing in the flume you know that the denser you pack filtering elements, the more flow (and particles suspended in it) will be deflected around the whole dendritic structure. So an extremely dense branching structure (a bush) is not optimal (no political statement implied). It would have a high encounter efficiency for those few particles that managed to find a way in, but your job is to maximize encounter rates. So being a great theoretician, you jump to the opposite extreme and (depending on how theoretical about dendritic extremes you want to get), you design a structure with no branches (a cylinder) or one branch (a "Y") or a "trifurcation" (as in the current variety of Bush). These structures have great encounter rate per filtering element, but there is (are) only one (or two or three) element(s), so the encounter rate at the level of the individual animal (whose ingestion rate is the issue) is lousy.

If you kept the flow velocity and particle concentration constant, you might be able to find an optimal branching pattern, or even switch to an array that is more regular (a grid or lattice) than a dendritic one. But this animal lives in the real world and since it is a (more or less) passive suspension feeder is stuck with a range of flow velocities and particle concentrations. Somewhere in a highly branching array under almost any conditions, a substantial proportion of the elements will be doing fairly well at encounter rates.

Not only suspension feeders are dendritic. Photosynthetic plants (*e.g.*, real bushes) need to encounter carbon dioxide and light. Think about rates of mass and energy transfer.

What next?

One of the things that is plain for flow carrying macroscopic particles past an appendages and that holds down to particles of about 1 μm in diameter is that in general there is only one encounter with each particle and hence only one try at catching it. (A few animals make vortices that will give them multiple chances at the same particle, raising efficiency but reducing the number of freshly arriving particles, so it is hard to argue for much gain in rate of encounter unless the vortex literally centrifuges the particles out onto an appendage.)

As the scale gets still smaller, however, molecular motions get much more rapid, but also much less unidirectional. Once a dissolved molecule hits an object the first time, it is likely to hit it many more times. Feeding by diffusion (thermally agitated motion) on dissolved molecules is thus well served by luring them close. The next big item that we will look at is diffusive transport of mass.

Readings

For sediment transport, there is no section in Vogel. For the mechanisms of suspension feeding, read pp. 355-360. A comprehensive review is available, but it is too long and technical to be a useful general reading for this class:

SHIMETA, J.S. AND P.A. JUMARS. 1991. MECHANISMS OF PARTICLE ENCOUNTER BY SUSPENSION FEEDERS. *OCEANOGR. MAR. BIOL. ANN. REV.* **29**: 191-257. (IF YOU WANT TO LOOK AT THIS REFERENCE, YOU CAN EASILY FIND IT ON MY WEBSITE.)

I WOULD ASK YOU INSTEAD TO RETURN TO DEVELOPING YOUR INTUITION FOR PROCESSES AT LOW *Re* IN PREPARATION FOR THE NEXT COUPLE OF WEEKS BY READING:

PURCELL, E.M. 1976. LIFE AT LOW REYNOLDS NUMBER. *AMERICAN JOURNAL OF PHYSICS* **45**: 3-11.

This paper has become a classic and is available on line at <<http://brodylab.eng.uci.edu/~jpbrody/reynolds/lowpurcell.html>>. I will be aiming mostly at the argument that bacteria can't raise their encounter rates with solutes by swimming through them.