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MECHANICAL DESIGN IN SEA ANEMONES

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INTRODUCTION

By applying principles of fluid and solid mechanics to biological structures, I have studied the morphological adaptations of two species of sea anemones to the mechanical activities they perform and the environmental forces they encounter. The two species of anemones I used represent different extremes in mechanical behavior: Metridium senile, a calm-water species noted for the great range of shapes and sizes it can assume (Batham and Pantin, 1950), and Anthopleura xanthogrammica, a species occurring in areas exposed to extreme wave action (Hand, 1956; Dayton, 1971). I chose anemones because they are simple in structure, thus differences in morphology and function between species are easier to recognize and characterize than they would be for more complex animals.

Which aspects of the structure of M. senile and A. xanthogrammica enable them to harvest food effectively from such different flow regimes while they withstand the associated mechanical forces? I expected these animals with the same basic body plan but with mechanically different life-styles to differ in structure on several levels of organization: 1) the materials level (the structure and composition of mesoglea), 2) the whole-organism level (the shapes and dimensions of bodies), and 3) the environmental level (the ways in which animals fit into their mechanical environments). The environmental level of organization is the topic of this paper. Sea anemones are sessile marine animals, thus water movement is the most important aspect of their mechanical environment. I expected the distribution, behavior, and structure of M. senile and A. xanthogrammica to determine the environmental mechanical forces they encounter.

FLOW CONDITIONS IN THE FIELD

By SCUBA diving and working low tides, I surveyed a number of sites along the coast of Washington to determine the characteristic habitats of M. senile and A. xanthogrammica and to observe their posturing and feeding behavior. I also measured water velocities in order to characterize quantitatively the flow regimes of localities where the two species occur as well as of their microhabitats within those localities.

M. senile are subtidal animals occurring on rock in areas exposed to steady tidal currents typically on the order of 0.1 $m \cdot s^{-1}$. These M. senile are tall (mean height above the substratum = 38.1 cm. standard deviation (SD) = 8.8, number of measurements (n) = 28) and thus are subjected to essentially mainstream current velocities (Figure 1). M. senile in flowing water are bent over (Figure 2); this bending orients their oral disks normal to the current. I have observed these anemones filtering zooplankton from the water passing through the meshwork of numerous small tentacles on their fluted oral disks. Gut content analyses confirm that M. senile are zooplanktivorous.

A. xanthogrammica carpet the bottoms of intertidal surge channels at rocky exposed coastal sites. At high tide they are subjected to the oscillating bottom flow as waves pass overhead; at low tide they are subjected to the shoreward surge and seaward backwash of waves breaking seaward of them. Mainstream velocities in surge channels are highest (often greater than 3 to 5 $m \cdot s^{-1}$)

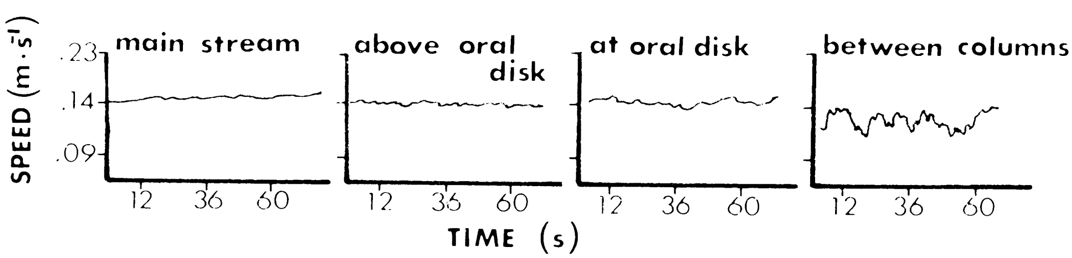

Figure 1. Water speeds measured using a thermistor flowmeter (LaBarbera and Vogel, 1976): "mainstream" = 60 cm above a bare vertical rock wall near a bed of M. senile; "above oral disk" = 10 cm above the oral disk of a M. senile 30 cm tall in the middle of the bed; "at oral disk" = 1 mm above the oral disk of the same M. senile; "between columns" = 20 cm above the substratum and 1 cm from the downstream side of the column of the same M. senile.

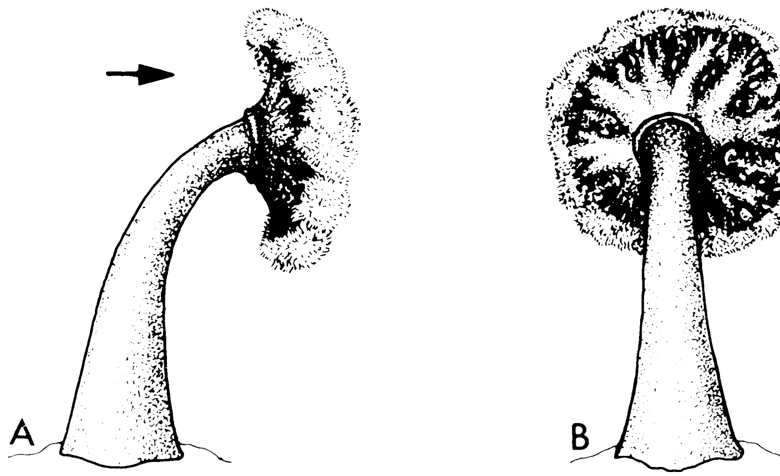

Figure 2. *M. senile* bent over in a tidal current. A. Side view (arrow indicates flow direction), and B. Rear view.

during surge and backwash; the mainstream flow (Figure 3) is bidirectional with a period of about 10 s. *A. xanthogrammica* in surge channels are short (mean height above the substratum = 2.5 cm, SD = 0.9, n = 71). Flow over these anemones (Figure 3) is more turbulent and of lower velocity (typically 1 $m \cdot s^{-1}$ maximum) than mainstream. Hence, unlike *M. senile*, *A. xanthogrammica* in essence hide from the maximum flow velocities which characterize the areas where they occur by being short.

A. xanthogrammica feed primarily on mussels which fall on the anemone's oral disks after being ripped off the substratum by starfish, logs, and waves (Dayton, 1973). I found greater current velocities higher in the intertidal. Mussels occur higher in the intertidal than do *A. xanthogrammica*, thus flow velocities are 3 to 5 times higher where the mussels are ripped off the rock than they are where the anemones must catch and hold on to them.

A few solitary *A. xanthogrammica* occur at sites exposed to lower flow velocities (maximum mainstream velocities typically 1 $m \cdot s^{-1}$) than those in surge channels. *A. xanthogrammica* in such protected areas are taller (mean height above the substratum = 7.1 cm, SD = 2.4, n = 25) than those in exposed channels and thus stick out into currents as rapid as those encountered by the short *A. xanthogrammica* in exposed channels. Thus, anemones from apparently different flow habitats are actually in similar flow microhabitats by virtue of their heights above the substratum. This illustrates that a knowledge of mainstream flow conditions does *not* tell us the flow regime encountered by a particular organism.

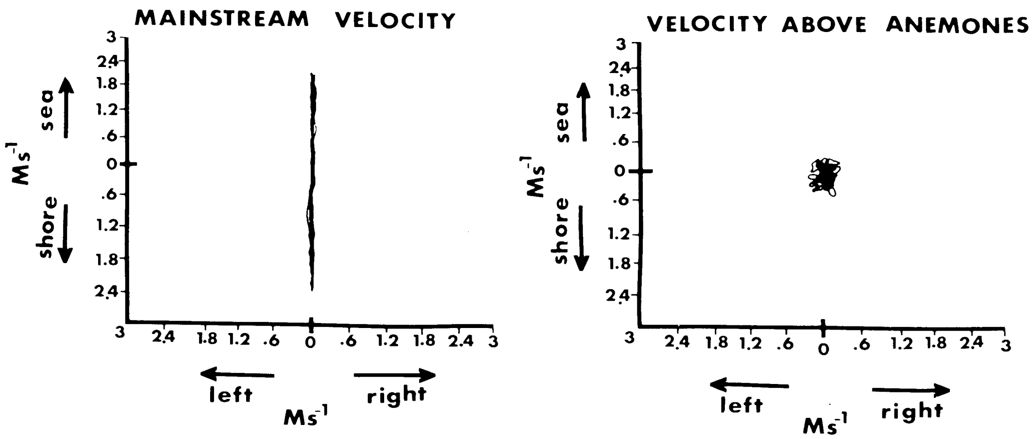

Figure 3. Flow velocities measured using an electromagnetic flowmeter (EPCO Model 6130) in a surge channel during surge and backwash: "mainstream" = 115 cm above the substratum; "above anemones" = 3 cm above the oral disk of an A. xanthogrammica surrounded by other A. xanthogrammica on the floor of the channel (Flow into ("shore") and out of ("sea") the channel is indicated on the vertical axis and flow from side to side ("right", "left") in the channel is indicated on the horizontal axis.)

DRAG FORCES ON ANEMONES

When fluid moves relative to an object, it exerts a force (termed drag) on that object tending to push the object downstream. Drag increases as velocity increases. Although A. xanthogrammica "hide" from mainstream currents and M. senile do not, A. Xanthogrammica encounter flow velocities generally an order of magnitude higher than those met by M. senile. I therefore expected the shapes of A. xanthogrammica to minimize drag more than those of M. senile.

I used my field measurements of flow velocities and of anemone body dimensions to calculate the drag forces on M. senile in tidal currents and A. xanthogrammica in waves. I calculated the forces on M. senile-shaped objects using the standard drag equations for cylinders in steady flow (Rouse, 1961). Calculation of the forces on A. xanthogrammica subjected to wave action is complicated by the fact that the water is continually accelerating and decelerating in different directions around these anemones. Fortunately ocean engineers have worked out a body of equations for predicting wave forces on pilings (Keulegan and Carpenter, 1958; Wiegel, 1964; Bretschneider, 1966). I used these equations to calculate the forces on A. xanthogrammica-shaped pilings in surge and backwash.

My calculations indicate that although M. senile occur in calm regions and A. xanthogrammica in exposed areas, the flow force on an individual anemone of either species is nearly the same (on the order of 1 N). Drag forces on A. xanthogrammica measured in the field are in fact typically 1 N (Koehl, in prep., a).

How can the drag on a M. senile in a 0.1 $m \cdot s^{-1}$ current be the same as the drag on a A. xanthogrammica in 1.0 $m \cdot s^{-1}$ flow? One way to minimize the drag on an object is to minimize the size of the wake that forms behind the object. One way to minimize wake size is to present most of the surface area of an object parallel to the direction of flow. (Think of the force on a flat plate oriented parallel to the current versus on one oriented normal to the current.) A. xanthogrammica in surge channels are short and wide (mean ratio of pedal disk diameter to height = 2.5, SD = 0.7, n = 70) hence most of their surface area is parallel to the direction of flow and drag is minimized. M. senile on the other hand are tall (mean ratio of pedal disk diameter to height = 0.3, SD = 0.1, n = 40), and are bent over in currents so that their large oral disks are oriented normal to the flow direction, hence drag is maximized. Flow tank measurements of drag on models of anemones in various configurations confirm that this effect of shape on drag is the case (Koehl, in prep.,a). Thus, the drag on an individual anemone of either species is essentially the same because of the respective shapes and orientations of the animals.

What types and magnitudes of stresses do such drag forces produce in the body walls of these anemones? (Stress is the force per cross-sectional area over which that force is distributed.)

DRAG-INDUCED STRESSES IN ANEMONE BODY WALLS

The shape of an animal determines the distribution of stresses within the animal for a given load distribution. The stiffness of the materials composing an animal determines how much the animal will deform in response to these stresses. Since the same load that causes a M. senile to bend over does not noticeably deflect an A. xanthogrammica, I predicted that the latter would have a more stress-minimizing shape and a stiffer body wall than the former.

A sessile anemone can be considered as a cantilever supporting a feeding apparatus in flowing water in the proper orientation for food-capture. A cantilevered beam (sea anemone) subjected to a load (drag) undergoes shearing and bending (Figure 4). The magnitude of the shearing stress produced in a beam by a given load depends upon the cross-sectional area of the beam, but is independent of the shape of the beam. The magnitude of tensile stress in a bending beam depends not only upon the cross-sectional area, but also upon the length and the shape of the beam (see Wainwright and Koehl,

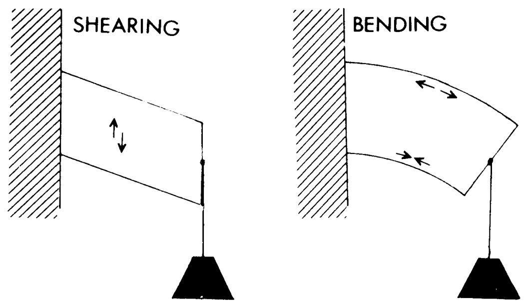

Figure 4. Deformation of a cantilevered beam supporting a load.

this symposium). The oral disk of an anemone deformed in shearing remains parallel to the substratum and the flow direction whereas the oral disk of an anemone deformed in bending will not. I have modelled sea anemones as continuously-loaded hollow cantilevers of the proper shape and have used beam theory (Faupel, 1964) to calculate the shear stresses and the tensile stresses associated with bending that environmental forces would produce in the body walls of M. senile and A. xanthogrammica.

The calculated shear stresses in a M. senile are on the order of 200 $N \cdot m^{-2}$ whereas the maximum tensile stresses associated with bending are on the order of 4,000 $N \cdot m^{-2}$. As expected, these maximum stresses occur at the narrow region of the upper column of a M. senile. It is not surprising that a M. senile in a current is bent at this upper region of its column; the anemone's filtering oral disk is thus oriented normal to the direction of flow and is held out in the more rapidly flowing water away from the substratum.

The calculated shear stresses and maximum tensile stresses in an A. xanthogrammica body wall are typically 120 $N \cdot m^{-2}$ and 100 $N \cdot m^{-2}$ respectively. Thus, although an A. xanthogrammica is exposed to wave action, because it is short and wide, the tensile stresses in its body wall due to flow forces are an order of magnitude lower that those in a tall, calm-water M. senile. A. xanthogrammica do not bend visibly in flowing water; their oral disks remain upright where mussels are more likely to fall on them.

The elastic modulus, or stiffness (see Wainwright and Koehl, this symposium), of A. xanthogrammica body wall is three times greater than that of M. senile body wall when they are stretched at biologically relevant rates (Koehl, in prep.,b). Thus, these two species of anemones differ in their mechanical response to flow not only because of their respective shapes, but also because of the materials from which they are built. Hence, the flexural stiffness, which depends upon both shape and material (see Wainwright and Koehl, this symposium), of A. xanthogrammica is two orders of magnitude greater than that of M. senile.

I used the same assumptions that I used in the above calculations to compute the deflections of the oral disks of individuals of each species when subjected to drag. Deflections predicted in this manner are consistent with deflections of the anemones observed in the field.

SUMMARY

Typical values for the current velocity, drag, stresses, flexural stiffness, and deflection of a M. senile and a A. xanthogrammica of the same pedal disk diameter (15 cm) are summarized in Table I.

The design of an organism can actually affect the flow forces it encounters as well as its response to those forces, as illustrated by the sea anemones M. senile and A. xanthogrammica. M. Senile occur in calm areas, but because they are tall, they are exposed to mainstream current velocities. Although A. xanthogrammica occur in areas exposed to wave action, they are short and effectively hide from mainstream velocities. Nonetheless, water velocities encountered by A. xanthogrammica are an order of magnitude greater

TABLE I

	Metridium senile	Anthopleura Xanthogrammica
TYPICAL VELOCITY	.1 $m \cdot s^{-1}$	1.0 $m \cdot s^{-1}$
FORCE ON AN INDIVIDUAL	.8 N	1.0 N
SHEAR STRESS	180 $N \cdot m^{-2}$	120 $N \cdot m^{-2}$
MAX BENDING TENSILE STRESS	4520 $N \cdot m^{-2}$	100 $N \cdot m^{-2}$
FLEXURAL STIFFNESS (EI)	.08 Nm^2	10.56 Nm^2
DEFLECTION OF ORAL DISK	7 cm	.0004 cm

than those met by *M. senile*. However, the drag force on an individual of either species is about 1 N due to the respective shapes of each species. Since the tensile stresses in a bending beam increase with the length and decrease with the diameter of the beam, these flow-induced stresses in the tall, slim *M. senile* are an order of magnitude greater than in the short, wide *A. xanthogrammica*. Not only are the tensile stresses greater in *M. senile*, but their body walls stretch more for a given stress than do those of *A. xanthogrammica*.

The water currents encountered by these anemones and their mechanical responses to the currents can be related to the manner in which the anemones harvest food from flowing water. *M. senile* bend over in currents and suspension-feed through their oral disks whereas *A. xanthogrammica* remain upright in surge and catch mussels which fall on their oral disks. I have used the case of these two species of sea anemones to illustrate the importance of water flow to sessile marine animals both in terms of their mechanical support systems and their mechanisms of feeding.

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