

HYDRODYNAMIC FORCES

BRIAN GAYLORD

University of California, Davis

Hydrodynamic forces represent the tendency of water to push on organisms as it flows past them. On rocky shores, these forces result primarily from fluid motions associated with ocean waves that break on the shore. Hydrodynamic forces can act in the direction of water motion, perpendicular to it, or even against flow, depending on the specific causal mechanism. Drag and lift constitute the dominant forces if the pattern of flow surrounding but outside the immediate vicinity of the organism is constant over time and space, whereas additional forces arise when patterns of flow vary. In all cases, magnitudes of hydrodynamic force depend on organism shape, size, and properties of the tissues from which a plant or animal is constructed. These forces can act as important agents influencing ecological processes in coastal marine communities.

GENERALITIES OF SHORELINE FLUID FORCES

Both gases and liquids are fluids and can impart forces when flowing past objects and organisms. In coastal marine habitats, the relevant fluids are largely air and seawater. However, because fluid forces scale in proportion to fluid density, and because the density of seawater is more than 800 times greater than that of air, hydrodynamic forces due to flowing seawater usually dominate over aerodynamic forces associated with wind.

The seawater flows that result in the largest hydrodynamic forces are produced by ocean waves as they approach and break on the shore, and to a lesser extent by surf zone currents, themselves often tied to wave conditions as well as changes in tidal elevation. Such flows can vary substantially in both space and time such that organisms may be subjected to multiple types of hydrodynamic force in short succession or even simultaneously.

DRAG

The most familiar hydrodynamic force is that of drag. Drag acts in the direction of flow and therefore tends to push organisms downstream. It arises due to a combination of two factors: skin friction and an upstream–downstream pressure difference. The skin friction component emerges as a consequence of the no-slip condition, which dictates that seawater in contact with the surface of an organism does not move relative to that organism. Because

seawater at other locations far from the plant or animal flows unimpeded, this means that in intervening regions closer to the organism, fluid layers must move relative to one another. Skin friction results from the fact that the viscosity of seawater resists such relative motion.

In many cases, particularly when seawater is flowing past a nonstreamlined organism, a wake may also be created behind a plant or animal. Wakes arise when the downstream contour of an organism is curved too sharply for the flow to follow along it, such that the fluid stops tracking the shape of the organism (it separates from it) and heads more or less directly downstream. This effect in turn creates a downstream region where fluid recirculates in vortices of a range of sizes. In such wake regions, pressures are typically lower, and in combination with higher pressures generated on the upstream side of the organism, lead to a net force directed downstream. This component of force is pressure drag (Fig. 1). For organisms with a sizable wake, pressure drag can greatly exceed the accompanying skin friction.

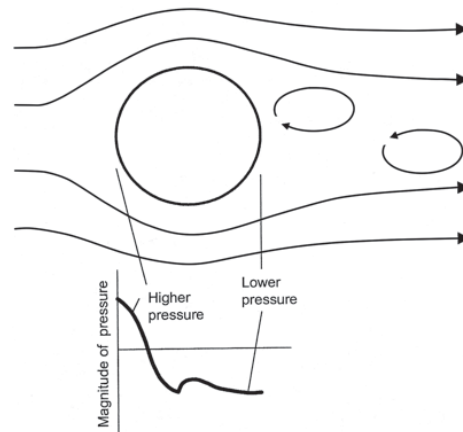


FIGURE 1 The pressure distribution around a circular cylinder produces pressure drag due to differences between above-ambient pressures upstream and below-ambient pressures downstream in the wake.

The difference between upstream and downstream pressures varies roughly with the square of the seawater's velocity relative to the organism, and because the pressure component often dominates, the total drag typically operates similarly. Pressure itself has units of force per area, which means that the total drag (F_D) also tends to scale in proportion to the area of the organism that faces into flow. Usually these relationships are expressed by means of the drag equation: $F_D = 1/2 C_D \rho S U_R^2$,

where ρ is the mass density of the fluid, S is typically the frontal area of the organism, U_R is the fluid's velocity relative to the organism, and C_D is the drag coefficient. A primary complication is that for streamlined organisms, an alternative convention for S is used (the wetted area = total surface area) because the lack of an appreciable wake means that friction over the full surface of the organism is more relevant for dictating the force than the area facing flow. The drag coefficient itself varies widely, depending on the shape of the organism as well as properties of the flow, as is discussed further herein.

LIFT

Lift, unlike drag, acts perpendicular to flow. It is the force that holds birds aloft, but it can also act horizontally or downward; its line of action simply depends on details of the flow pattern around an organism. Lift arises from differences in pressure between two sides of an organism as induced by differences in flow speed. Fluid traveling around an organism (or an organism's body part, for that matter) often must travel faster around one side than the other, to rejoin smoothly at the organism's downstream edge. Due to a physical rule called Bernoulli's principle, regions of flow characterized by high velocities tend to be accompanied by low pressures, and vice versa. As a consequence, whenever there is asymmetry in the split paths that fluid takes in passing around an organism, there is a capacity for a lift force to be produced, directed laterally toward the side of the organism that experiences the faster flow. Everyday examples include bird wings or fish tails, where fluid travels at a more rapid rate around their convex sides than their flat sides, as shown in Fig. 2.

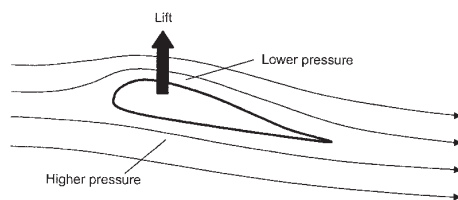


FIGURE 2 Top versus bottom asymmetries in flow around a bird wing or fish fin (represented schematically in cross section here) produce lift, directed perpendicular to the arriving flow.

Although such lift forces can act on the fins of fishes and appropriately shaped sedentary marine organisms, there is another, somewhat different class of lift that may operate more routinely in shoreline habitats. This force is near-wall lift. In the case of organisms that live

attached to the substrate, seawater cannot flow readily around all sides of their bodies because of their positioning against the rock. Nonetheless, there can still be mechanisms by which pressure gets transmitted to the substrate side of the organism, which can enable a net lift to be induced. Flow past the limpet shown in Fig. 3 provides an example: As seawater speeds up in passing over the elevated shell of the animal, this causes a reduction in pressure above it. At the same time, beneath the limpet, the imperfect seal of the shell against the substrate enables seawater to seep under its edge, whereby it moves inward against the animal's body and upward against the shell's underside. The net result is a relatively high internal pressure that is not fully counteracted by the lower pressure outside. The pressure mismatch can lead to a tendency for the limpet to be pulled away from the rock.

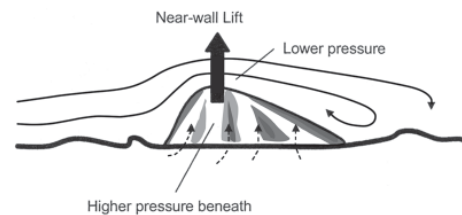


FIGURE 3 Near-wall lift acts on a limpet as higher-pressure seawater seeps under the shell and lower pressure, faster flowing seawater passes over it.

Both classes of lift forces (F_L) are related to flow speed in much the same way as drag and can be expressed via an analogous lift equation: $F_L = 1/2 C_L \rho S U_R^2$. Thus, lift, like drag, increases with the square of the speed of the fluid relative to the organism. In this case, however, S is typically taken to be the planform area: the area one would see if viewing the organism along the line of action of the lift force, oriented perpendicular to the incident flow. C_L is the lift coefficient, another index of shape that usually does not equal C_D .

FORCES TIED TO CHANGES IN VELOCITY

Drag and lift are potentially present in all flows. Additional hydrodynamic forces, however, arise if flow fields vary in time or space. The first of these forces results from the pressure gradient that intrinsically accompanies an accelerating parcel of fluid. The second derives from a mass of fluid immediately adjacent to the organism that alters the organism's interaction with the rest of the flow. A third force arises when an air-sea interface,

for example, that associated with the leading edge of a breaking wave, impinges on an emergent plant or animal.

Virtual Buoyancy

Basic physics dictates that a parcel of seawater (which has mass) can accelerate only if a larger force is imposed on one side than the other. The effects of such a difference in force, however, are also transferred through the interior of the parcel such that a pressure gradient arises within it. An organism immersed in this pressure gradient will experience a net force due to seawater pushing harder on one side than the other (Fig. 4). This force is often termed virtual buoyancy because it is related to the familiar buoyancy force that arises in a stationary column of fluid as a result of the vertical pressure gradient induced by gravity. Virtual buoyancy acts in the direction of fluid acceleration and is quantified using the expression $F_{VB} = \rho V A$, where V is the volume of the organism and A is the acceleration of the fluid relative to the earth. Note that this relationship means that if the fluid is decelerating, virtual buoyancy acts—nonintuitively—opposite to the direction of fluid movement. Virtual buoyancy is independent of the shape of an organism.

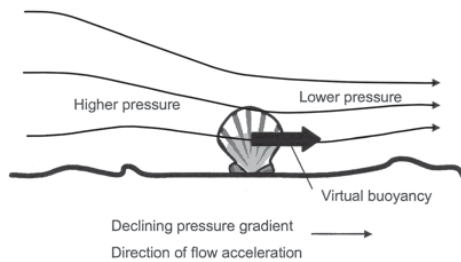


FIGURE 4 Virtual buoyancy as imposed on a scallop attached to the rock. The relationship of this force to buoyancy proper can be observed by mentally rotating the page 90 degrees counterclockwise. Then the acceleration-associated pressure gradient becomes directly analogous to the standard gravitationally induced one characteristic of a stationary body of water, where pressure increases with depth and produces an upward force on any immersed organism (realized as flotation).

Added Mass Force

Another force arises in association not with how a flow changes in an absolute sense but with how it changes with respect to an organism. Seawater in the vicinity of a plant or animal is influenced by the organism and thus moves differently than fluid farther away. Indeed, there is a mass of fluid (the added mass) that behaves in

a physical sense as if it were attached to the organism. The consequences of this added mass can be evaluated from two perspectives. In considering situations where seawater accelerates past a stationary organism, the added mass can be understood in terms of its tendency to cause the organism to displace more of the surrounding fluid than it would otherwise. This effect results in the imposition of an added mass force (F_A) that, in direct analogy to virtual buoyancy, arises as a consequence of the pressure gradient tied to the accelerating flow (Fig. 5A). A second perspective pertains to situations where the organism itself accelerates (Fig. 5B). Under these circumstances, assuming the fluid does not accelerate at the same rate as the organism, the added mass acts like an additional mass over and above the organism's own body mass. This mass provides extra resistance to acceleration, thereby functioning effectively as an opposing force. In both of these two acceleration scenarios, the added mass force is expressed as $F_A = C_A \rho V A_R$, where C_A is the added mass coefficient, another shape factor, and A_R is the acceleration of the fluid relative to the

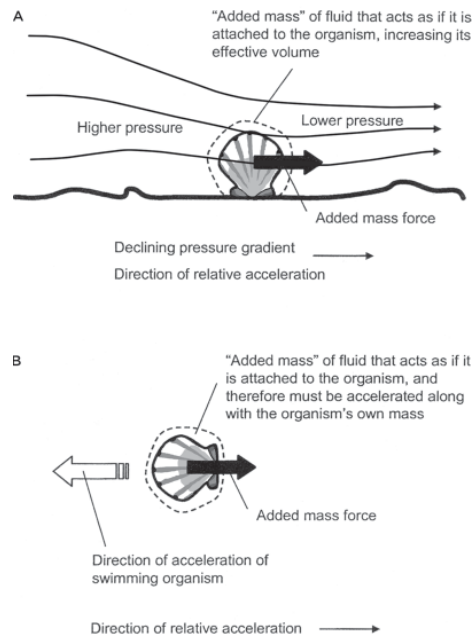


FIGURE 5 The added mass force as imposed on an attached or free-swimming scallop. (A) When seawater accelerates past a stationary organism, the added mass increases the effective volume of the organism, which results in a supplementary virtual buoyancy-type force. (B) If the same organism were to itself accelerate relative to flow, the added mass acts like extra mass to retard the acceleration, functioning in the same way as a force directed opposite to the acceleration.

organism. It may also be noteworthy that the added mass force is sometimes termed the acceleration reaction, whereas on other occasions the sum of the virtual buoyancy and added mass forces are lumped together under this name.

Impingement Force

A third force associated with changes in velocity arises when the air–sea interface of the leading edge of a breaking wave directly impacts a plant or animal. In this case, there is a sudden need for moving seawater to shift its trajectory (i.e., decelerate and shift laterally to establish a new flow pattern) to pass around the organism. This deceleration requires a force, which is provided by the presence of the organism. Naturally, the flow pushes back, and this response produces the impingement force. Recordings on rocky shores suggest that this force, although often lasting only very briefly, can be among the largest imposed on surf zone organisms.

EFFECTS OF SIZE AND FLOW SPEED— THE REYNOLDS NUMBER

One of the major complications in estimating magnitudes of hydrodynamic force derives from the difficulty of determining the three force coefficients: C_D , C_L , and C_A . There are a number of reasons for this difficulty, but paramount among them is that these coefficients are not constants but depend on aspects of the flow.

The drag coefficient, for example, is a function not only of an organism's shape, but also of a parameter called the Reynolds number. The Reynolds number is defined as $Re = \rho U_R L / \mu$, where ρ is again the mass density of the fluid, μ is its viscosity, U_R is the velocity of the fluid relative to the organism, and L is a length term that characterizes the size of the organism, usually its maximal length along the axis of flow. The Reynolds number represents the relative importance of fluid inertia versus viscous effects in a flow: At high Re , the flow has a tendency to maintain its original trajectory and frictional effects are relatively minor, whereas at low Re , the flow is less resistant to directional or speed changes and frictional processes become more important. In the surf zone where seawater is the primary fluid of interest, differences in Reynolds number are equivalent to differences in flow speed for a given organism of fixed size.

In general, skin friction is a greater fraction of the total drag at low Re than at high Re . Furthermore, skin friction depends more on the relative velocity than it does on the square of relative velocity. To account for this feature, the

drag coefficient varies essentially as $1/U_R$ at low Re . This pattern can be seen in Fig. 6, which depicts the C_D of a smooth sphere as a function of Reynolds number. This graph also serves as a reminder that identical organisms in different fluids (each characterized by a ρ and μ), or identically shaped organisms of different sizes (as indexed by L), can have distinct drag coefficients because of the consequent change in Re .

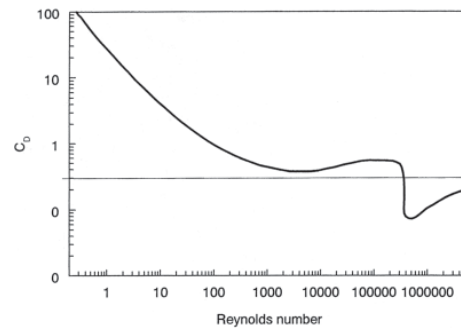


FIGURE 6 The drag coefficient for a smooth sphere as a function of Reynolds number. The sudden decrease (the drag crisis) at $Re = 3 \times 10^5$ reflects an abrupt downstream shift in the location where flow separates from its rear side.

In some cases, shifts in the drag coefficient with Reynolds number can be dramatic. For instance, a drag crisis occurs with smooth spheres and cylinders at around $Re \sim 10^5$ such that the flow very near their surfaces, in what is called the boundary layer, switches abruptly from a smooth state in which mixing is nearly absent to a turbulent state in which tiny swirls, vortices, and eddies are produced. These turbulent motions enable the point of separation along the contour of the sphere or cylinder to slide further around to the rear (Fig. 7). This process in turn dramatically reduces the size of the wake and thus the drag coefficient. Although most organisms have surfaces that are sufficiently rough that analogous drag crises do not arise in nature, there is at least one curious example of a situation where it does (Denny 1989).

The lift coefficient and added mass coefficient depend, as well, on aspects of flow. The lift coefficient, in particular, becomes increasingly minuscule at low Reynolds numbers. Lift coefficients are also strongly influenced by the orientation of an organism or its body part with respect to the arriving flow. A fish fin tilted moderately relative to the incident flow, for example, can have a large lift

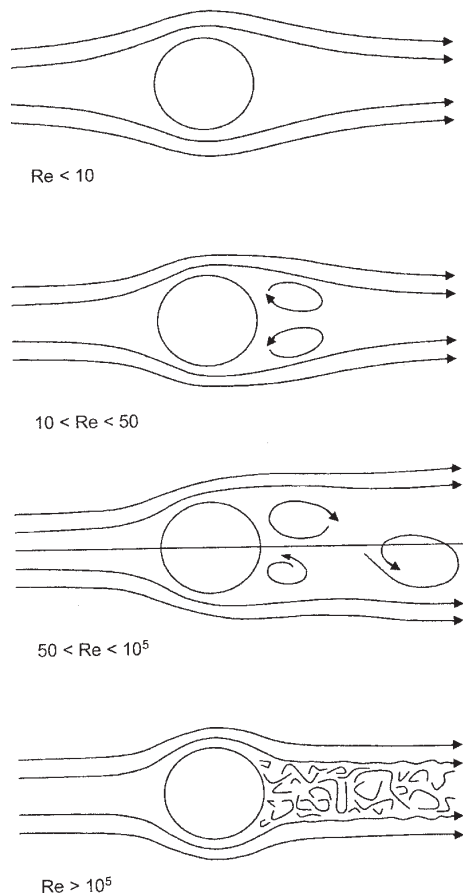


FIGURE 7 Representative flow patterns past a circular cylinder oriented perpendicular to the direction of fluid movement, as a function of Reynolds number. At low Re , flow passes smoothly around the cylinder and, although there is upstream-downstream asymmetry, no obvious wake is apparent. At somewhat higher Reynolds numbers (10–50), stable recirculating vortices form behind the cylinder. For $50 < Re < 10^5$, these vortices are shed alternately from one side then the other, creating a vortex street. At higher Re yet, the wake narrows and becomes turbulent, characterized by disorganized fluid motion with considerable mixing. Note that the numerical values given are approximate and can vary within a factor of 2–5 as a function of conditions in the incident flow.

coefficient, whereas the same structure inclined at either a lower or sharper angle may exhibit a smaller or even zero lift coefficient. The added mass coefficient can vary in bidirectional flow as a function of the distance of travel of the fluid past the organism before the flow reverses.

TISSUE PROPERTIES AND FORCE

There is a further complication that arises when estimating the hydrodynamic forces imposed on actual

shoreline organisms. Many, if not most, intertidal plants and animals are not entirely rigid. Flexible seaweeds, for instance, readily reorient and reconfigure in flow, with fronds compressing together as velocities increase. As a consequence, their drag coefficients become strong functions of flow speed when computed—as is the convention—relative to constant reference areas (usually the maximal frontal area that could face flow if the organism were held upright). Stiffer organisms naturally do not exhibit the same degree of conformational change as compliant ones and so show less of a decline in drag coefficient with flow speed. In this regard, the tissue properties of plants and animals influence their interaction with flow and thereby the hydrodynamic forces they experience.

The fact that flexible organisms such as seaweeds move passively in response to seawater motion has two other implications as well. First, in longer organisms that not only compact in flow but also sway or flop back and forth, a tendency to move with the fluid can reduce the speed at which seawater translates relative to an organism. This behavior decreases the velocity term in the drag equation and thus the applied force. Second, as an organism moves, it acquires momentum. This momentum can cause an organism attached to the rock to impose a force on itself as it reaches the end of its range of motion and is jerked to a halt. Interactions among these various effects indicate that flexibility has both advantages and disadvantages. In some cases, flexibility may result in a reduction in drag coefficient and decreased relative velocities, whereas in other cases it may elevate an organism's vulnerability to whiplash-type effects.

HYDRODYNAMIC FORCES ACROSS TIME AND SPACE

A number of the hydrodynamic processes identified previously can operate in concert on rocky shores and will sum together to impose an overall force. The relative magnitudes of the total and individual forces, however, can change as the tide rises and falls. At low tide, hydrodynamic forces are entirely absent over much of the shore. At intermediate tidal levels, waves begin to arrive at locations where organisms were previously emergent, and can crash directly onto them to impose impingement forces. At high tide, organisms often become completely immersed such that drag and lift become the major forces, and those from impingement disappear. It is also the case that magnitudes of total force are modulated

over longer time scales. Storms, for instance, produce large waves that chronically increase the severity of the flows faced by organisms. Both major and minor storms may be more likely during certain seasons of the year, or during specific years characterized by unusual weather patterns.

Hydrodynamic forces are also linked to geometrical features of the shore. At small scales, crevices and holes can provide protection from rapid water motions. Similarly, organisms low against the rock or behind upstream protrusions can exist in regions where average velocities are slower. Such plants and animals exploit the fact that velocities are reduced within and immediately adjacent to the roughness elements that make up the rugosity of the substrate. At the same time, at the scale of meters, velocities are often increased where topographical features accelerate flows, such as within converging channels aligned with the direction of wave travel, or along the sides of boulders where the flow speeds up to pass around them. At larger scales, coastal features such as headlands can focus waves and increase their sizes, leading to faster wave-generated water velocities and larger hydrodynamic forces.

COMMUNITY IMPLICATIONS OF HYDRODYNAMIC FORCE

Patch Formation in Space-Limited Habitats

A primary motivation for understanding hydrodynamic forces derives from the important roles they play in coastal communities. Lift, for example, can act to create new open patches in shoreline mussel beds. It arises because faster flows and lower pressures above the bed go unmatched by slower velocities and higher pressures in interstices within the bed (Fig. 8). The initiation of

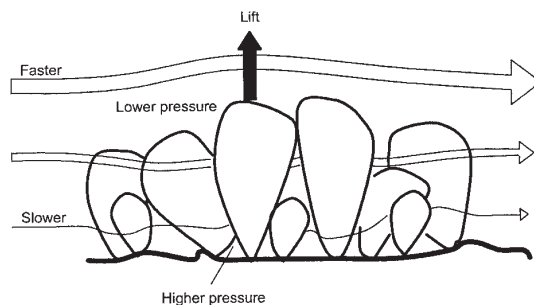


FIGURE 8 Lift can function as an important agent initiating patch removal in mussel beds, arising due to the combination of higher pressures in slower flow regions within the interstices of the bed and lower pressures in faster flow areas above the bed.

open patches is particularly relevant in coastal areas of the Northeast Pacific where mussels are often a dominant space occupier, growing in such densities that they form extensive beds composed of multiple layers of individuals. Because unclaimed rock substrate is commonly a limiting resource in these habitats, without the removal of mussels the amount of free space decreases and the abundance of other plants and animals declines. By removing mussels, therefore, hydrodynamic forces enable inferior competitors that would otherwise be excluded from a population to persist within it. A classic example is the sea palm (Fig. 9). This seaweed operates as a “fugitive” species in that although any specific individual lives only a transient existence in its own slowly disappearing patch, the species as a whole can reliably maintain a presence in the community by exploiting a continually changing assortment of open patches within the mussel bed.



FIGURE 9 Open patches in mussel beds provide substrate for the sea palm, a Northeast Pacific seaweed species found only on outer rocks subjected to large hydrodynamic forces imposed by breaking waves. Photograph by the author.

Effects on Food Supply and Consumption Rates

Hydrodynamic forces and the rapid flows that produce them can also carry dislodged organisms to nearby locations where they may become food for other shoreline animals. For instance, sedentary sea anemones that live on the bottom of surf zone pools acquire a majority of their sustenance from mussels, snails, and other animals that are knocked off the rocks and fall within the grasp of their tentacles. In much the same way, the fronds of many tattered or dislodged seaweeds are washed onto the beach where they provide fodder for a variety of sand-dwelling grazers (Fig. 10).



FIGURE 10 Dislodged seaweed individuals and fragments, washed onto the beach near Santa Barbara, California, following a storm accompanied by large waves. Such material provides food for many beach-associated grazers. Photograph by the author.

In other situations, hydrodynamic forces alter rates of acquisition or consumption of the food items that become available. For instance, barnacles may retract their feeding appendages when hydrodynamic forces exceed a given threshold. Other organisms that cannot hide their feeding structures may instead be bent over in response to hydrodynamic forces. Such changes modify the orientation of body structures that may be used for food collection and can thereby alter rates of food acquisition and consumption. Hydrodynamic forces can also affect the feeding strategies of animals with nonsedentary lifestyles. For instance, sea stars, voracious predators on many rocky shores, reduce their foraging activity when subjected to large waves.

Scaling Considerations

Different hydrodynamic forces also have the potential to be more or less important for small or large organisms. Both drag and lift depend on an area term, either the frontal area, the planform area, or the wetted area. In contrast, virtual buoyancy and the added mass force depend on an organism's volume. Because factors that vary in proportion to volume increase more rapidly with increases in size than do factors that vary with area (that is, as L^3 vs L^2 , where L is a characteristic length of the organism), one would expect that the latter two forces would become increasingly important relative to drag or lift as plants or animals get bigger.

Virtual buoyancy and added mass forces may indeed be the dominant ones that act on exceptionally large

organisms such as massive corals growing in deeper shoreline habitats exposed to nonbreaking waves (Massel and Done 1993). By contrast, however, volume-dependent flow forces do not appear to be more important for most surf zone organisms subjected to breaking waves. In these latter habitats, the spatial dimensions over which velocities vary are sufficiently small that individual accelerating parcels of fluid are unable to encompass the full bodies of larger organisms. Because virtual buoyancy and added mass forces each depend on the volume of the organism enclosed in the accelerating parcel of fluid, this characteristic limits the magnitude of force that can be imposed. As a consequence, acceleration-dependent forces in surf zone habitats do not appear to become large relative to drag and lift, even in bigger organisms.

On the other hand, momentum-related forces produced when flexible organisms reach the ends of their ranges of motion tend to vary in proportion to an organism's mass. Mass itself also increases with size in much the same way as volume. This relationship suggests that momentum-related forces should become disproportionately important relative to area-dependent fluid forces as flexible organisms get bigger. The capacity of such forces to outweigh drag and lift in large individuals, however, has not been fully explored.

SEE ALSO THE FOLLOWING ARTICLES

Body Shape / Buoyancy / Disturbance / Size and Scaling / Surf-Zone Currents / Wave Forces, Measurement of

FURTHER READING

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