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# Survival in the Surf Zone

## *Random properties of ocean waves combined with measurements of physical strength predict optimal sizes for wave-swept organisms*

Mark Denny

To a physicist hoping to establish a law of nature, random behavior in a natural system is a delightful thing. The predictive power of gas laws, for instance, arises from the random motion of gas molecules: Moving at a speed dictated by temperature, they collide occasionally and rebound in unpredictable directions, like so many tiny billiard balls. If gases acted in even a slightly less random fashion on the molecular level (which they do at very low temperatures), the behavior of a gas in bulk would be much more complicated, and gas pressures would be hard to predict.

Outside basic physics, however, examples of purely random behavior are rare. Take weather, for example; ironically, it cannot be predicted accurately because it is not unpredictable enough. The progression of weather from day to day involves both stochastic (random) behavior by atmospheric systems and a historical component: Yesterday's weather affects today's. The historical influence, a lack of day-to-day independence, vexes weather forecasters.

But there is at least one case in which "weather"—or more precisely, the variation of the environment in which organisms live—is so thoroughly unpredictable over the short term that its long-term effects can be predicted accurately. That is the environment creat-

ed where an ocean interacts with a shore in the surf zone. As we shall see, waves in near-shore waters operate sufficiently randomly over the short term that robust statistical techniques provide an accurate prediction of their long-term effects. Furthermore, the wave climate profoundly affects the distribution and abundance of plants and animals that inhabit the shore. This combination of predictable "weather" and its effects on organisms presents an opportunity to explore an interaction between biology and a physical environment.

### **Surface Waves**

Waves on an ocean's surface arise primarily from the action of wind. Air blowing over a sea exchanges some of its kinetic energy with the water below, thereby raising waves. Faster wind that has a longer time to interact with an ocean produces larger waves. Typically, waves are created continuously over large expanses of ocean surface, and wave height—the vertical distance between a wave crest and the preceding trough—varies gradually from place to place because of varying wind strength.

Once produced, a wave travels freely, often for very long distances. The large waves that batter the northwest coast of the United States, for instance, are often produced by storms far out in the northern Pacific Ocean or in the Gulf of Alaska. In an extreme example, the exceptionally large waves that destroyed the breakwater at Long Beach, California, on an otherwise sunny and calm day in 1930, arose thousands of miles away in a storm in the Southern Hemisphere.

As waves travel, their form changes subtly. Waves of different periods (the time from crest to crest) travel at different speeds and lose energy at different rates. In practice, travel removes

the short-period waves that are typical of locally produced "seas," and long-period "swells" are retained. The period of ocean swells typically varies from six to about 20 seconds. As a wave approaches shore and enters shallow water, its speed of travel decreases and its height grows gradually. As a result, a wave becomes steeper and more peaked, and at some point it becomes unstable and breaks. Such tall, breaking waves interact with organisms on the shore.

### **The Random Sea**

The plants and animals of wave-swept shores clearly inhabit a physically stressful environment, where waves break over them every half-dozen seconds or so. Nevertheless, the communities of wave-swept shores represent some of the most diverse and productive ones on earth. The challenge of explaining such rich biological diversity in the face of physical adversity arouses considerable interest, leading investigators to explore how plants and animals have been designed through the course of evolution to cope with the exigencies imposed by breaking waves.

Three relations play particularly important roles in an organism's interaction with a wave-swept environment. First, there is a basic consideration of population dynamics: Larger organisms are more likely to produce more young, leaving a greater relative contribution to the next generation. Second, larger organisms face a greater risk of being broken by a wave. Combining the first and second relationships raises a basic question of organismal design: How large should a wave-swept plant or animal grow? A smaller organism faces less chance of wave-induced breakage, but it will probably produce fewer offspring. A larger organism, on the other hand,

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Martin H. Chester (Photo Researchers, Inc.)

**Figure 1. Wave-swept organisms endure harsh environmental conditions. A crashing wave comes ashore every dozen or so seconds, and wave size varies randomly from moment to moment. In fact, the randomness of wave heights allows for predicting the long-term interaction between organisms at a shore and the physics of ocean waves, shown here at California's Big Sur.**

might be broken by a wave before it has a chance to reproduce, in which case its fitness is nil. Some size offers an optimum balance between survival and reproductive output. At that size, an organism just withstands the largest force imposed during its reproductive lifetime.

That leads to the third relation: The larger the waves that crash on a shore, the larger the hydrodynamic forces imposed on an organism. As a result, the wave climate sets the size that balances survival and reproductive output for a wave-swept organism. The maximum size of waves at a particular site should

allow predictions of the optimal sizes of plants and animals. But how large is the largest wave? Therein lies the utility of random behavior.

The waves crashing in a given surf zone probably originated in a wide variety of locations. Although most waves have a similar period (from six to 20 sec-

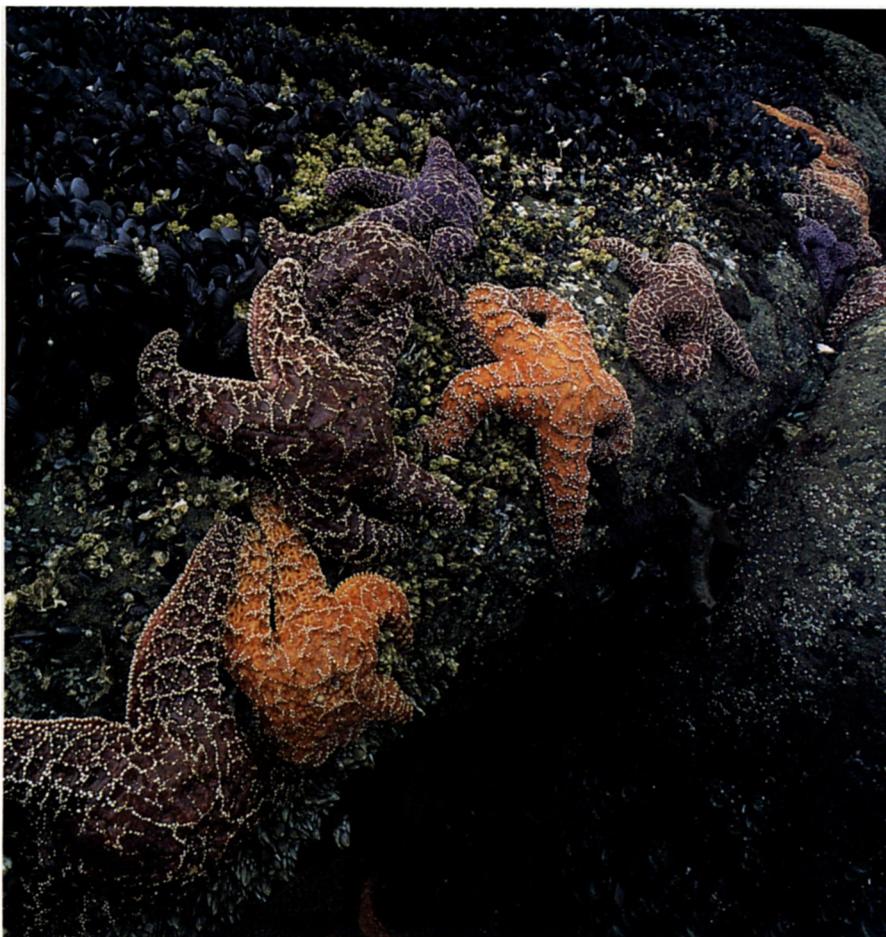


Figure 2. Diverse and productive communities of organisms inhabit shorelines, despite the environmental constraints. These mussels and sea stars, for instance, must be designed to survive the repeated impact of breaking waves.

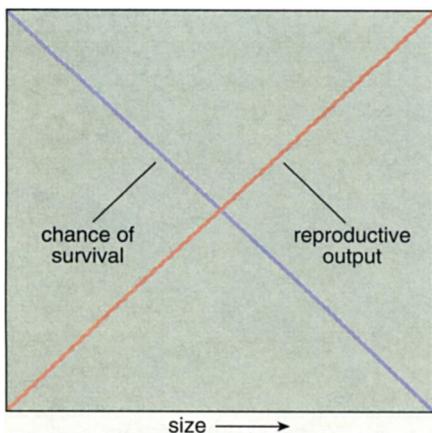


Figure 3. Size of a wave-swept organism represents a balance between competing factors. First, as an organism grows larger, its chance of surviving decreases, because it is more likely to be broken by a wave. Second, larger animals tend to produce more offspring. A successful shore organism balances these factors, growing large enough to produce as many offspring as possible, but remaining small enough to withstand the largest wave that it is likely to encounter. This illustration provides only a schematic representation of the relations; actual curves may be more complex.

onds), they rarely arrive at a shore in lockstep. The arrival of two wave crests on shore at the same time is a matter of pure chance. It is just as likely that a crest from one wave will arrive with the trough of another. In fact, waves arriving at a shore are likely to be assorted randomly in terms of their phase.

To a first approximation, ocean waves are additive. Where two wave crests coincide, the height of the resulting wave equals the sum of the heights of the individual waves. Likewise, a smaller wave results when a wave crest overlaps a wave trough. Waves of similar period but random phase combine at a shoreline through such processes. The resulting modulation of wave heights produces a condition called the "random sea," and the height of an individual wave arises from a random interaction among waves. As a result, predicting the height of individual waves proves impossible in practice.

The short-term stochastic behavior of wave heights might seem problematic for studying design constraints for

organisms on a shore. If individual wave heights are unpredictable, how can a biologist predict the height of the largest wave? The answer lies in a calculation made over a century ago by John William Strutt, Lord Rayleigh.

### The Cocktail-Party Paradox

As part of an extensive theoretical treatment of the physics of sound, Lord Rayleigh explored what might be called the "cocktail-party paradox." Imagine being at a party with 50 other revelers, each chatting away at the top of his or her lungs. It seems entirely possible that the peak pressure of each person's sound wave could reach your ear at the same time. The resulting pressure—a sound 50 times as loud as the average party sound—could potentially rupture your eardrum. How is it that cocktail parties do not result in widespread hearing damage?

Rayleigh solved this paradox by considering the superposition (algebraic addition) of a large number of sound waves of the same period but random phase. Like ocean waves, sound waves combine and modulate, and Rayleigh's calculations led him to propose the probability distribution known appropriately as the Rayleigh distribution. According to the Rayleigh distribution, the most common waves reaching a partygoer's ear have a slightly less-than-average amplitude. Waves with amplitudes above average do exist, but their probability decreases rapidly with increasing amplitude. In fact, you would have to attend cocktail parties continuously for over two years to encounter a sound even five times louder than average.

The same mathematics applies to ocean-surface waves. Waves of random phase reaching shore modulate each other, which produces a Rayleigh distribution of wave heights. In other words, an organism on shore must wait a long time, on average, to be subjected to the forces of an exceptionally large wave. Oceanographers quantify waviness with the so-called "significant wave height," essentially an average of the one-third tallest ocean-surface waves. A typical significant wave height on the West Coast of North America, for example, is about 2.3 meters. By knowing the significant wave height, one can generate a Rayleigh distribution that predicts the largest wave that is likely to crash on a given shore over a specific period of time.

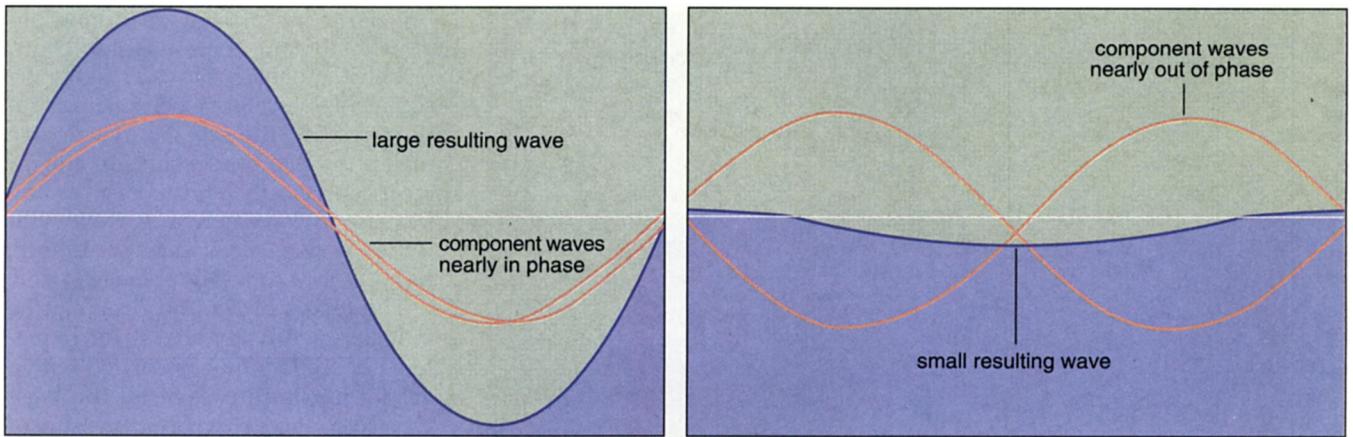


Figure 4. Ocean waves interact. If two waves (coral lines) from different places arrive at a shore nearly in phase (left)—crests and troughs aligned—the resulting wave (blue line) is larger, essentially the algebraic sum of the two component waves. The arrival of two waves out of phase, however, leads to a smaller wave hitting shore, because the components cancel each other (right).

An ocean's waviness, however, varies with time. During stormy periods, the near-shore significant wave height can be quite large. Significant heights greater than 10 meters have been recorded on the Oregon coast. Fortunately, the Army Corps of Engineers, in collaboration with the California Department of Boating and Waterways and the Scripps Institution of Oceanography, maintains a series of wave sensors along the coasts of California, Oregon and Washington. Measurements of significant wave height are taken four times each day, providing the basis for calculating the annual average. From these data, one can calculate a probability function that describes the variation in significant wave height along the entire coast, or a so-called wave-exposure distribution, which is a statistical description of how waviness varies over time.

The wave-exposure distribution found on the West Coast suggests that the largest wave likely in one year is approximately 5.9 times the yearly average significant wave height. So for a yearly average significant wave height of 2.3 meters, the largest wave likely to strike the shore in a year is approximately 13.6 meters high, or the height of a four-story building.

#### Wave Forces

Being able to predict the maximum wave height makes it possible to proceed with predictions of survival and optimal size for wave-swept organisms. The first step consists of connecting wave height to hydrodynamic forces. Knowing a wave's height allows the calculation of its velocity and acceleration. These values can then be

used to calculate the hydrodynamic forces that an organism experiences.

Wave height correlates with the velocity imparted to the water beneath its crest. In deep water, water beneath a crest moves at a small fraction of the velocity at which the wave travels. As water depth decreases during a wave's run toward shore, the speed of a wave form decreases, but the speed of water moved by the wave increases. At the breaking point, water in a wave crest moves at the same speed as the wave. Shortly after breaking, when a wave form has slowed still further, water in the crest can move even faster than the wave, which forms the plunging wave crest commonly depicted in surfing magazines.

Crest velocities of breaking waves can be surprisingly high and depend on the height of the wave and the depth of water. According to wave theory, a breaking wave 2.3 meters tall

should travel at a speed of 6.7 meters per second (about 15 miles per hour), and water at its crest would move at the same speed. In a breaking wave with a height 5.9 times the yearly average significant wave height of 2.3 meters, the wave and the water in its crest would travel at about 16 meters per second (about 36 miles per hour).

Waves in a surf zone are also accompanied by rapid water accelerations. As a wave breaks, its ordered motion degenerates into turbulence, and eddies flow across the seabed. A rough consideration of the size of these eddies and the rate at which they are moved by a wave leads to predicted accelerations that increase with wave height, and may reach 1,000 meters per seconds squared in some areas. Values in excess of 400 meters per seconds squared have been measured on wave-swept rocky shores. These are extreme-

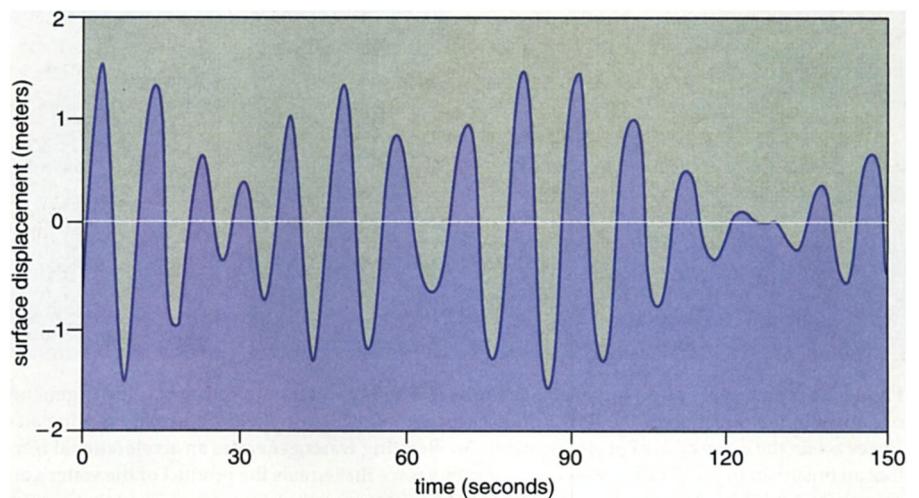
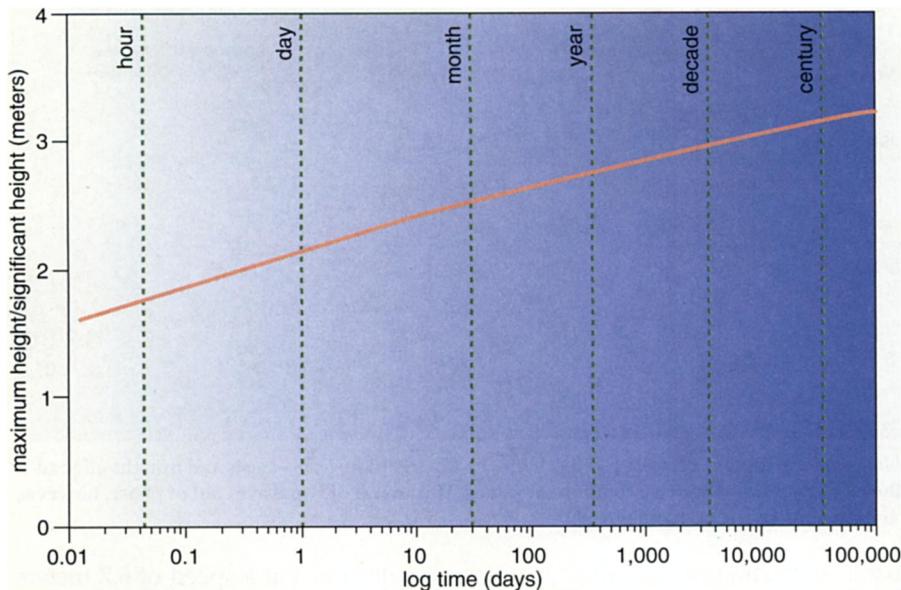


Figure 5. The "random sea," random variations in the height of an ocean's surface at a given point over time, arises from interactions of ocean waves.



**Figure 6.** Height of the largest wave likely to hit a shore increases predictably with time, according to a theoretical extension of the Rayleigh distribution and the assumption that the significant wave height remains constant. Oceanographers quantify waviness on the basis of significant wave height, the average height of the largest third of all waves. The ratio of maximum wave height to significant wave height increases gradually with time, shown here on a logarithmic scale. In any hour, for instance, the maximum wave hitting a shore will probably be less than twice as big as the significant wave height. And about a century passes before a wave three times higher than the significant wave height hits a shore.

ly high accelerations (40 to 100 times the acceleration of gravity), much higher than those found in almost any other aquatic environment.

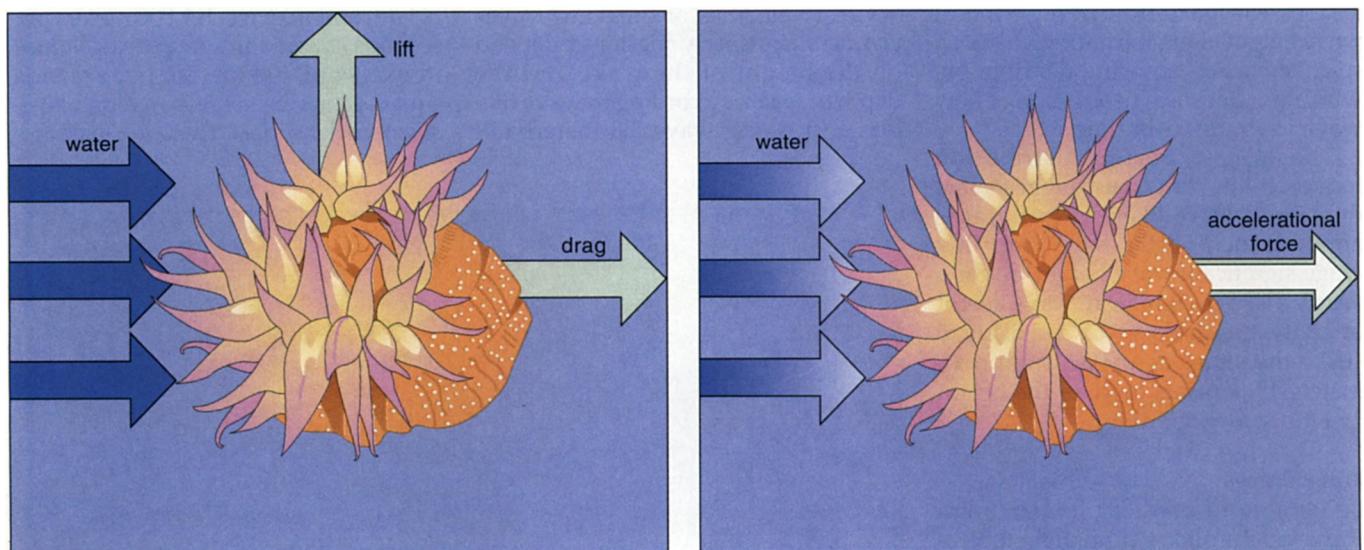
Both the velocity of water and its acceleration impose forces on objects embedded in the flow. Velocity generates

two types of force: drag and lift. Drag acts on the area of a plant or animal exposed to the flow and tends to push an organism downstream. Lift also acts on an organism's exposed area, but it tends to pull the organism across the flow, typically away from the substra-

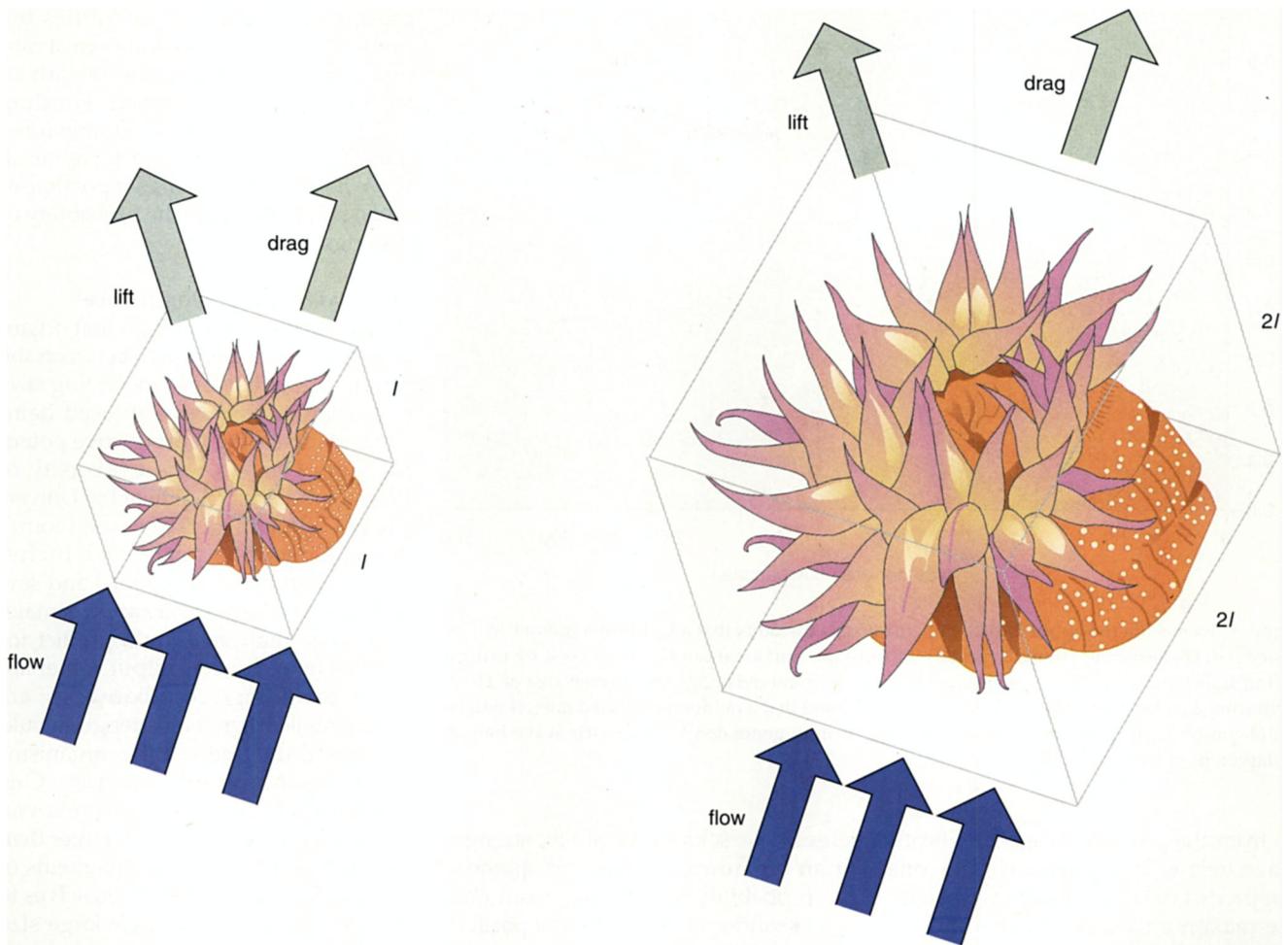
tum. Both drag and lift are proportional to the dynamic pressure of the flow, or half the density of water times the square of the water velocity. Being proportional to the square of velocity makes these forces sensitive to any increase in velocity, and thereby to any increase in wave height. A wave with twice the average velocity, for instance, imposes four times the average force.

The forces of lift and drag can be quite large. A water velocity of 16 meters per second, that associated with a yearly maximum wave off the West Coast, produces a dynamic pressure of 130,000 pascals. Applying the same pressure over the projected area of a human body would be equivalent to about 13 metric tons. This helps explain why survivors of a ship wrecked on a rocky coast do not decide lightly to swim ashore.

Size also plays a fundamental role in hydrodynamic forces. Doubling the linear dimensions of an organism, for example, quadruples its exposed area, thereby quadrupling the drag and lift experienced from a given velocity of water. The ability of an organism to resist hydrodynamic forces, however, increases similarly with size. The strength of an animal or plant increases approximately with the cross-sectional area of its skeleton or with the area of its adhesive apparatus. So as an organism grows larger, its ability to resist forces



**Figure 7.** Several forces affect organisms in the surf. Moving water with constant velocity generates two forces: drag and lift (*left*). Drag pushes an organism in the direction of the flow, and lift acts perpendicular to the flow, usually pulling an organism away from the substrate. Both of these forces act on the exposed area of an organism. Accelerating water generates an accelerational force (*right*). Newton's second law of motion dictates that an organism in accelerating water experiences a force that equals the product of the water's acceleration and the mass of water displaced by the organism. Actual measurements of accelerational force (*gray arrow*), however, exceed that predicted by Newton's second law alone (*white arrow*). The accelerating water changes the pattern of water flow around an object, and the rate of change develops a force that enhances the overall accelerational force. The magnitude of an accelerational force depends on an organism's volume, rather than its area.



**Figure 8.** Size determines the effect of wave-induced forces. Imagine an organism that is essentially cube-shaped. If a cube's side is  $l$  units long (left), then it has sides with area  $l^2$  and an overall volume of  $l^3$ . Increasing an organism's linear dimensions by a factor of two (right) produces sides with area  $4l^2$  and an overall volume of  $8l^3$ . Given that drag and lift increase with an organism's frontal area and that an organism's strength is probably related to its attachment area, which increases similarly, an organism's risk of drag- or lift-induced dislodgment or breakage does not increase with size. Accelerational force, on the other hand, depends on an organism's volume, which increases faster than strength as an organism grows. This scaling problem could determine the size at which an organism breaks.

increases in proportion to the drag and lift it feels, because both are proportional to area.

Nevertheless, the force due to acceleration upsets the balance between applied force and strength. Unlike drag and lift, the accelerational force is proportional to an organism's volume, not its exposed area. Consequently, doubling an organism's linear dimension results in an eightfold increase in accelerational force, causing it to increase faster than an organism's strength, which makes a larger organism more likely to be dislodged. This accounts for the size-specific risk proposed above in considering the optimal size of wave-swept plants and animals.

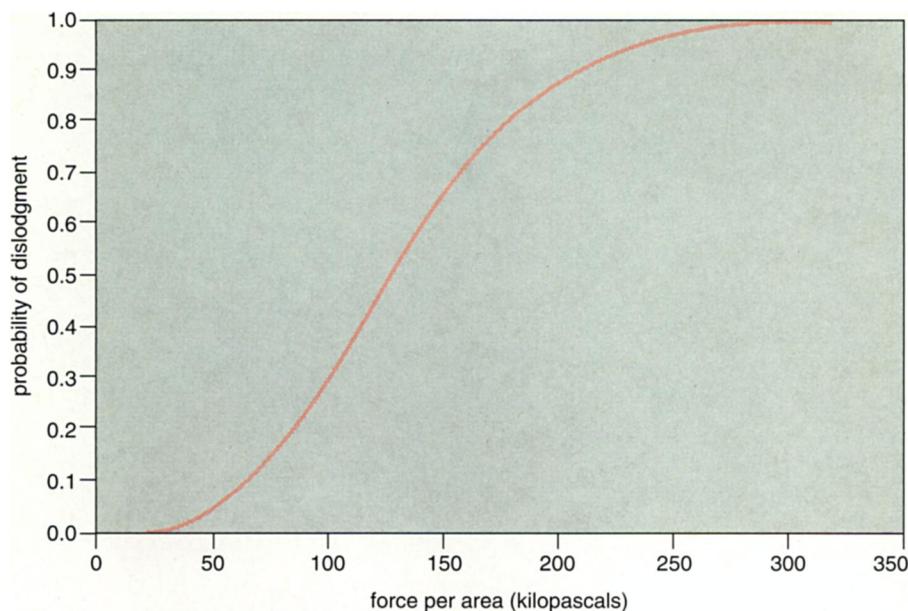
#### Side Effect of Shape

Beyond size, an organism's shape affects hydrodynamic forces, and therein

lies the potential for an adaptive response by an organism to its environment. In many cases, that response takes place through the course of evolution. Hydrodynamic forces have apparently affected the evolution of rigid skeletons of some sea urchins, including the shingle urchin (*Colobocentrotus atratus*), which possesses reduced spines and a streamlined shape. It inhabits wave-swept shores in Hawaii, where it is commonly found fully exposed to the breaking swell. Another urchin (*Echinometra mathaei*) inhabits the same shores, but it has the more typical pincushion appearance of a sea urchin that leads to higher drag, perhaps explaining why it typically lives in cracks and crevices that are shielded from the waves. In other cases, adaptation develops from a physiological response during growth. Some algae, for

instance, can be induced to grow with a streamlined shape by hanging small weights from their fronds to mimic the force of drag.

Theoretical predictions of the relation between biological shape and flow-induced forces remain difficult, so it is common practice to measure directly the proportionalities between velocity or acceleration and force when dealing with wave-swept organisms. A plant or animal can be attached to a force transducer and exposed to a carefully controlled flow in a flume or a wind tunnel. By varying the speed and acceleration of the flow, the resulting forces can be measured. Using these values, one can calculate the force that a given organism experiences when subjected to a given water velocity and acceleration, and thereby the force associated with a wave of a given height.



**Figure 9.** Increasing the applied force per area boosts the odds that a California mussel will be dislodged. Dislodgment strength (pascals, or force per unit area) can be determined by using a spring scale to measure the force required to dislodge a mussel occupying a given area of a bed. Collecting data for many mussels reveals the likelihood that a randomly selected mussel will be dislodged by a given force per area, or the lift or drag generated by a specific wave height. (Adapted from Denny 1993.)

So from the yearly average significant wave height for a particular site, one can predict the maximum wave height, the maximum water velocity and acceleration and the maximum force imposed on an organism.

What risk does this force impose on an organism? Here again, theory provides little practical utility, so we resort to empirical measurements. Organisms of a range of sizes can be broken using a force transducer, and the relations among a species' size, shape and strength can be ascertained. In general, considerable variation in strength exists among individuals of a species. As

a result, we seldom specify *the* strength of an organism. Instead, we quantify the probability that an organism chosen at random has less than a particular strength.

Consider the strength of attachment in California mussels (*Mytilus californianus*). At Tatoosh Island, a site on the coast of Washington, 178 mussels were dislodged from the substratum, and the force was measured with a spring scale. These force values can be normalized by dividing them by the size of the dislodged mussel, expressed in this case as the area that the mussel occupies in the bed. Ranking these normalized values

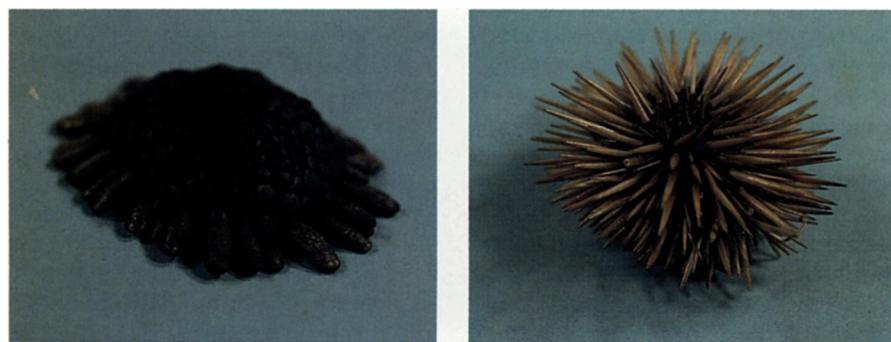
produces a curve that quantifies the probability that a mussel, chosen at random, will be dislodged when a particular force per area is applied. For drag and lift, force per area is a simple function of water velocity and therefore of wave height, which makes it possible to relate wave climate to the probability of dislodgment.

### Optimal Size and Dominance

Preliminary studies suggest that organisms may strike a balance between the counteracting effects of increasing size: increasing risk of wave-induced damage and increasing reproductive potential. Tom Daniel of the University of Washington, Mimi Koehl of the University of California, Berkeley, and I found that the common purple sea urchin (*Strongylocentrotus purpuratus*) and several species of limpets are approximately the size that one would predict for optimal reproductive output. Other animals, including acorn barnacles, are much smaller than their strength would allow, and the size of these organisms must depend on other factors. One species of coral, fire coral (*Millepora complanata*), grows substantially larger than we predicted, but broken fragments of this species can recement themselves to the reef and grow. So their large size could be a strategy for dispersal and vegetative reproduction.

A more compelling case for the effect of hydrodynamics on optimal size may exist in algae. Although the abundant algae of wave-swept shores are blade-like and bend in flow to assume a streamlined shape, Brian Gaylord of Stanford University and Carol Blanchette of Oregon State University showed recently that the shapes of several macroalgae tend to trap water within a frond's interstices, thereby magnifying the apparent volume of a plant. As a result, the accelerational force on an alga may be an order of magnitude larger than that on an animal of equal mass. Hydrodynamic-based predictions of the size at which three species of wave-swept macroalgae should achieve their maximal reproductive output closely matched the sizes observed in nature.

Beyond reproductive output, knowledge of maximal wave height may also explain the competitive allocation of space on the substratum. The California mussel, for instance, dominates mid-intertidal, rocky shores from Alaska to central California. Although starfish prey on these mussels in the low-inter-



**Figure 10.** Organisms can adapt to forces by changing shape. The shorter, more streamlined spines of a shingle sea urchin (*left*), for example, allow it to inhabit wave-swept shores in Hawaii. A neighboring species (*right*) bears the standard pincushion of spines that generate more drag, which relegates that species to cracks and crevices along the same shores. (Photographs courtesy of the author.)



Figure 11. Mussel dislodgment helps to determine the makeup of ecological communities along rocky mid-tidal shores from Alaska to central California. When not disturbed, California-mussel communities display wall-to-wall coverage. Waves can uproot sections of mussels, producing bare spots that can be colonized by invading species, including algae, as shown here. (Photograph courtesy of C. A. Blanchette.)

tidal zone and desiccation prevents them from inhabiting the high-intertidal zone, they form densely packed beds at mid-tidal levels. This dominance potentially excludes other species, thereby reducing the species richness of mid-intertidal shores. Knowledge of the maximal wave heights on these shores may help explain the competitive allocation of the substratum.

Although not prone to biological disturbance, mussels in the mid-intertidal zone can be dislodged by waves. Breaking waves during winter storms, for instance, rip out areas of mussel beds. A variety of algae and invertebrates quickly colonize the patches of open substratum. As mussels reclaim open patches, other patches are formed by more waves, resulting in an ever-shifting interaction among the rates of patch formation, colonization and reclamation.

The resulting community depends on the rate of mussel dislodgment. A high rate of dislodgment results in a large fraction of the substratum being available for colonization by competi-

tive subordinates and a relatively long period in which a given patch is likely to remain mussel-free. In such a case, subordinate species interact freely, much as they would in the absence of mussels. A low rate of dislodgment produces short-lived bare patches, and only rapidly colonizing species can survive.

What rate of mussel dislodgment does a statistical approach predict? Using the mussel strengths determined at Tatoosh Island and the significant wave height of 2.3 meters from nearby sites, I predict that about 6.4 percent of the mussels will be dislodged on average. In an 11-year study of the dynamics of open patches at this site, Robert Paine of the University of Washington and Simon Levin of Princeton University recorded average dislodgment rates of from 6.3 to 12.3 percent, comfortably close to the value predicted by theory.

The predicted rate of dislodgment is quite sensitive to waviness at a site. If the yearly average significant wave height is only 2.0 meters, I predict that only four percent of the mussels will

be dislodged in a year, opening approximately four percent of a mussel bed for colonization. If, on the other hand, the yearly average significant wave height is three meters, then my measurements predict that 14 percent of the mussels will be dislodged. Therefore, a one-meter variation in yearly average significant wave height would result in nearly a fourfold variation in the rate at which bare space is created in mussel beds. In fact, data over a 37-year period in the North Sea reveal that yearly average significant wave height there varied from 1.0 to 1.8 meters around a long-term mean of about 1.4. Such a variation of more than 50 percent of the mean could have drastic consequences for intertidal communities.

Fundamental principles of ecology lie beneath the seeming disarray of waves crashing against a shore. A combination of statistical analyses and empirical measurements suggests that an organism in the surf zone often grows large to enhance its reproductive potential, but not so large that it cannot survive the largest wave that it is likely to encounter during its life. So the short-term stochastic properties of ocean waves provide an excellent arena for exploring the long-term interaction between the physics of the surf zone and the size and strength of wave-swept organisms.

#### Acknowledgments

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