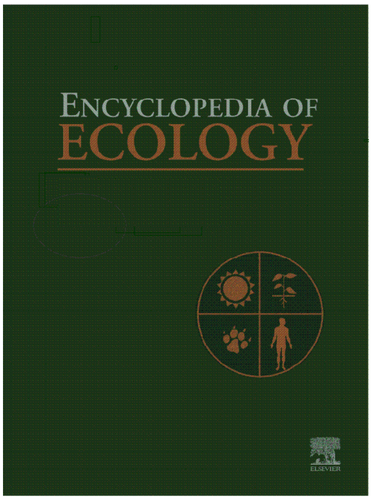

C A Blanchette, M J O'Donnell, and H L Stewart. Waves as an Ecological Process.
In Sven Erik Jørgensen and Brian D. Fath (Editor-in-Chief), Ecological Processes.
Vol. [5] of Encyclopedia of Ecology, 5 vols. pp. [3764-3770] Oxford: Elsevier.

$$\mathrm{cwt}(f)(a,b) = \int f(t)\psi(at+b)\mathrm{d}t$$

In cwt, a wavelet ψ is dilated and translated by any real value a and b. In discrete wavelet transform (dwt), however, a wavelet ψ is dilated and translated by only discrete values. Often we use powers of 2 dilation (called dyadic):

$$\psi(2^k t + l)$$

where k and l are integers. The dwt of f is a function of scale 2^k and time l given by

$$\mathrm{dwt}(f)(2^k, l) = \int f(t)\psi(2^k t + l)\mathrm{d}t$$

Orthogonal wavelets are discrete wavelets which lend themselves to very fast algorithms to compute dwt.

See also: Application of Ecological Informatics; Hopfield Network; Multilayer Perceptron; Simulated Annealing.

Further Reading

Chui CK (1992) *An Introduction to Wavelets*. Boston: Academic Press, (volume 1 of a new series).

Daubechies I (1988) Orthonormal bases of compactly supported wavelets. *Communications in Pure and Applied Mathematics* 41: 909–996.

Daubechies I (1992) *Ten Lectures on Wavelets*. Montpelier, VT: Capital City Press.

Iyengar SS, Cho EC, and Phoha VV (2002) *Foundations of Wavelet Networks and Applications*. New York: Chapman and Hall.

Holmes CC and Mallick BK (2000) Bayesian wavelet networks for nonparametric regression. *IEEE Transactions on Neural Networks* 11: 27–35.

Mallat SG (1989) A theory for multiresolution signal decomposition: The wavelet representation. *IEEE Transactions on Pattern Analysis and Machine Intelligence* 11(7): 674–693.

Mallat S (1998) *A Wavelet Tour of Signal Processing*. New York: Academic Press.

Ruskai MB, Beylkin G, Coifman R, *et al.* (1992) *Wavelets and Their Applications*. Boston: Jones and Bartlett.

Stollnitz E, DeRose T, and Salesin D (1996) *Wavelets for Computer Graphics*. San Francisco: Morgan Kaufmann Publishers.

Strang G (1989) Wavelets and dilation equations: A brief introduction. *SIAM Review* 3(4): 614–627.

Strang G and Nguyen T (1996) *Wavelets and Filter Banks*. Wellesley: Wellesley Cambridge Press.

Strichartz R (1994) Construction of orthonormal wavelets. In: Benedetto J and Frazier M (eds.) *Wavelets*, pp. 23–50. Boca Raton, FL: CRC Press.

Sweldens W (1995) The lifting scheme: A construction of second generation wavelets. Technical Report, 1995: 6. Columbia: Industrial Mathematics Initiative, Department of Mathematics, University of South Carolina.

Szu H, Telfer B, and Garcia J (1996) Wavelet transforms and neural networks for compression and recognition. *Neural Networks* 9: 695–708.

Zhang Q and Benveniste A (1991) Approximation by nonlinear wavelet networks. *International Conference on Accoustics, Speech and Signal Processing* 5: 3417–3420.

Waves as an Ecological Process

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Wave Mechanics

Of the physical process in the ocean, ocean waves are perhaps the most visible to the casual observer. The surface of the ocean is rarely still; slight puffs of wind send small ripples across still water. On exposed coasts, little ripples are usually unnoticed as walls of water rear up from the undulating sea surface and fling themselves against the shore with crashing roars and showers of foam. In shallow habitats, waves can exert an important influence on the distributions of organisms.

Waves on the surface of the ocean get their energy from wind blowing over the top of the water. As air moves over the water, friction causes the water to pull in the same direction, forming small ripples. With time and distance, little ripples become larger ripples and eventually form large waves, which can travel far from the location where they were originally formed. Actually, the idea of a wave traveling needs some explanation: waves are a rhythmic displacement of the surface of the water. The water itself moves in an elliptical pattern, and an individual particle of water returns to almost the same spot at the top of each wave. The waveform itself travels across the surface; what is really moving is the energy of the wave passing through the water. A wave can be described by several parameters: its wavelength, which is the distance between two subsequent peaks; its period, the time it takes for a complete wave cycle; and its amplitude, the vertical distance

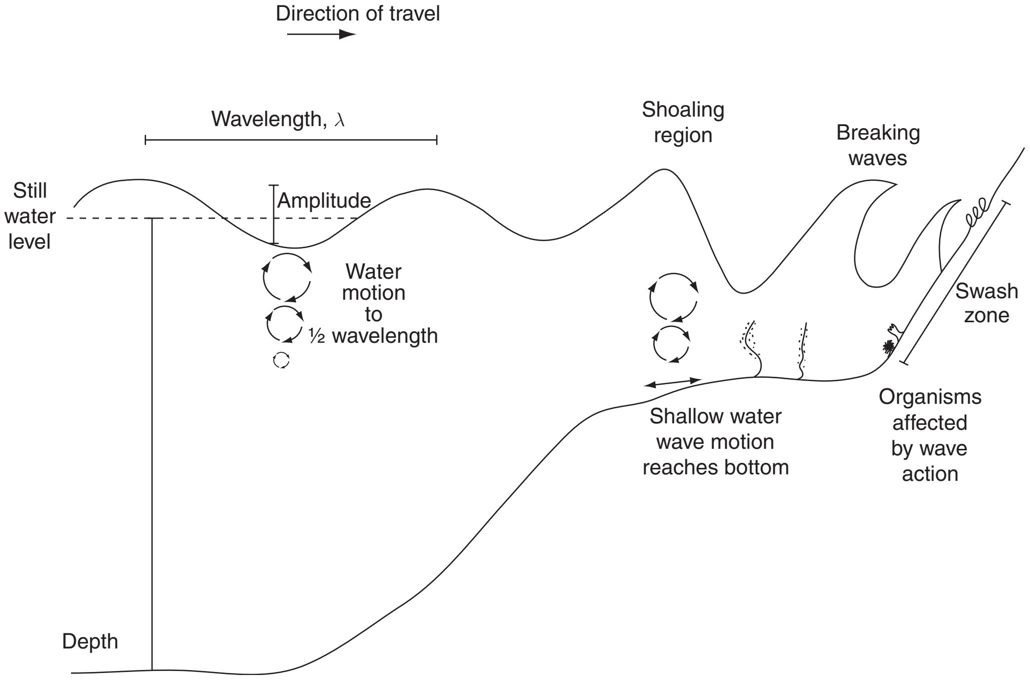

Figure 1 Anatomy of a wave. Draft by Michael O'Donnell.

between the peak and the trough of a wave (**Figure 1**). Waves travel across the ocean with some speed, known as the celerity. The disturbance of waves does not just occur at the surface; water beneath the surface is also moving in an orbital path, with smaller and smaller orbits until the depth of the water is half of the wavelength.

Once formed, ocean waves can travel long distances with very little dissipation. This means that storms in the middle of the Pacific Ocean send waves to both California and Japan. As they enter shallow water (where the water depth is less than half the wavelength), waves begin to change; the orbital motion of the water interacts with the bottom to become more elliptical. As a result, waves in shallow water undergo a process known as shoaling, becoming taller and steeper. In this region near the shore, waves begin to interact with the communities of organisms living on the bottom, subjecting them to oscillatory water motion. Over soft bottoms, waves will form ripples in the substratum, which help to structure the habitable space.

In very shallow water waves become so steep that they can no longer maintain their shape. The water below the wave is being slowed by drag on the bottom to a greater extent than the water at the top of the wave. At this point, the top portion of the wave will tumble over and begin to break. During breaking, all of the energy of the wave is dissipated in the turbulent motion of water on the shore. Breaking is a violent process, and can result in very high water velocities and high levels of turbulence. Most of the energy of breaking waves is expended in the intertidal zone and the shallow subtidal region. For organisms living in these regions on wave-swept shores, waves are one of the dominant features of their physical environment.

Life in the Wave-Swept Environment

The most direct mechanism by which waves influence populations is by removing or destroying individual organisms that live on wave-swept shores. The velocity of the water beneath shoaling and breaking waves can impose large forces on biological structures in their paths. The primary forces of moving fluid over a stationary object are lift and drag. Both of these forces increase with the velocity of the fluid squared, which means that a small increase in water velocity leads to a large increase in the force that an object experiences. The velocities beneath breaking waves can be very high (investigators have measured velocities in excess of 30 $\mathrm{m\,s^{-1}}$), as can the forces exerted on organisms living beneath breaking waves. For an organism of the size of a golf ball on a moderately wave-swept shore, this can translate into forces as high as 200 N (~20 kg) that the organism must resist if it is to remain on the shore.

In coastal ocean regions, waves can impose large hydrodynamic forces on benthic organisms. If the forces imposed by waves are larger than the attachment to the substratum (tenacity) or the mechanical strength of organisms, they may become broken or dislodged (**Figure 2**). The tenacity of mobile animals is often

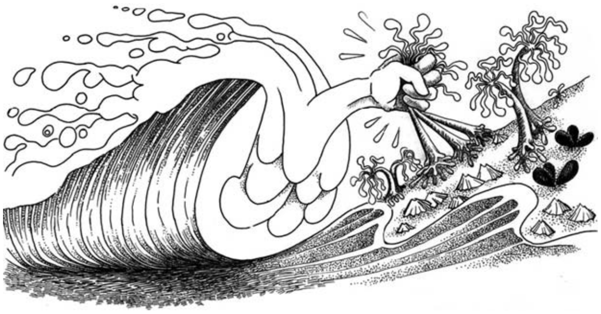

Figure 2 Cartoon representing the opposing forces of drag imposed by waves resisted by the strength and tenacity of benthic organisms. Cartoon by Jeffrey Harding.

Figure 3 Seabirds running on beach. Photo courtesy of Callie Bowdish.

reduced when they move, raising the possibility that predators and grazers increase their risk of dislodgement when they forage. Breakage and dislodgment does not always lead to death; some organisms can regenerate broken parts or, if dislodged, may be able to re-attach and grow at another location. This may be an effective mechanism of dispersal for organisms that live in extremely wave-swept environments. For a large number of organisms, dislodgment does lead to death and several researchers have been experimenting with predictive models to describe survivorship as a function of wave height. These models are becoming more refined over time as more data become available to strengthen the link between wave height and maximal water velocity.

Strategies for Survival in the Wave-Swept Environment

From coral reefs to temperate intertidal rocky shores to sandy beaches, waves shape near-shore marine communities through interactions with individual organisms. The high energy of water moving in waves has important implications for wave-exposed organisms. There are several ways marine organisms deal with waves.

Behavioral Strategies

Mobile organisms in wavy habitats may time their forays into wave-swept areas to calm periods or high tide when the effect of the waves is less intense. For example, crabs on rocky shores walk around and forage between waves but grab on and assume a low, flattened posture that minimizes drag when waves hit. Seabirds run out of the way of waves as they forage in the swash on sandy beaches (Figure 3), and burrowing invertebrates dive down into sand to find refuge from waves deep down in between sand grains. Not all organisms avoid waves, however. Seals and dolphins can be found surfing in waves and killer whales have been reported to use the froth of breaking waves as camouflage for hunting seals on the beach.

Strategies of Sessile Organisms

Benthic sessile organisms that cannot move out of the way of wave action use a number of strategies that enable these organisms to withstand the forces imposed on them by waves.

Strength

Strength is a common strategy for persisting in wave-swept habitats. The strength of the attachment (by holdfasts of algae, byssal threads in mussels, and foot size in snails) of organisms exposed to waves is often higher than in calm habitats. Barnacles, snails, and limpets also have strong shells, which protect them against wave action. By retracting into their hard, strong shells, these animals can protect their soft bodies from the high energy of waves breaking directly on them. On coral reefs, the strength of scleractinian (reef building) coral skeletons enables them to thrive under waves breaking on the reef. The strong, stiff structures of corals enable them to resist forces from all directions imposed by waves. Many corals are strong enough to withstand the hydrodynamic forces that they experience in waves, and the substratum to which corals are attached often breaks before the coral itself.

Flexibility and elasticity

Another strategy for surviving waves is to be flexible. Flexible organisms do not require resources for structural support; therefore, this may be a less costly alternative than strength for survival in wavy habitats. Seaweeds provide a good example of this approach. Flexible algae are easily reconfigured into streamlined shapes by water moving around them. This reduces the force exerted on an alga by decreasing the area exposed to hydrodynamic forces. A flexible organism may also be pushed easily down toward the substratum where flow velocities are reduced by interactions with the benthos. A flexible organism can be reconfigured and pushed in alternating directions by the bidirectional flow of waves. The back-and-forth motion of flexible organisms in waves may also rub them against the adjacent substratum. This may damage the organism itself, but can also dislodge potential neighbors and keep the area around it free from competitors. Back-and-forth motions of flexible organisms in waves can also act to dislodge epibionts such as snails or epiphytic algae. These riders may prey upon the organism or may compete with it, as do epiphytic algae competing for light or nutrients with their host alga.

Another approach to survival in waves is used by the alga *Postelsia palmaeformis*. This alga resembles a small palm tree and stands upright, often sticking up in the air (**Figure 4**). It thrives on the most wave-exposed areas in temperate intertidal zones, where individuals are knocked over by almost every wave. The stipe (equivalent to terrestrial plant stalk) of *Postelsia* is flexible and highly elastic. In combination with the shape of the stipe, this allows this alga to rebound back into an upright posture after it is pushed over by a wave and the wave has passed. In this way *Postelsia* thalli are reconfigured into streamlined shapes and pushed down toward the substratum where water velocities may be reduced, but they then passively spring back to upright postures by energy stored in their resilient stipes, much the same way an elastic band rebounds back into shape after being stretched. Similarly, other algae rely on buoyancy to return them to their upright postures after waves have pushed them over. Such algae are pushed against the bottom by waves, and then passively return to an upright position by the upward force of buoyancy when the flow slows.

Size and numbers

A flexible organism can survive waves by moving along with the flow. This strategy is effective for long organisms, such as kelps. By being longer than the displacement of the water in a wave, such kelps can avoid experiencing high hydrodynamic forces associated with waves. While the kelp moves along at the same velocity as the water in the wave, it experiences no water motion relative to its surfaces, and therefore no force. When the water in the wave reverses direction, the kelp is passively carried along with the water motion in the other direction. If the kelp never becomes completely strung out in one direction before the water velocity of the wave reverses, it can avoid the high forces associated with waves. In this way, large flexible, weak organisms can persist in areas exposed to waves.

Figure 4 The sea palm, *Postelsia palmaeformis*. Photo by Carol Blanchette.

Small size is also thought to be a characteristic of organisms exposed to waves and, indeed, many of the organisms persisting in wave-swept habitats are small (e.g., many seaweeds, barnacles, snails, and limpets). Organisms capable of altering aspects of their morphology often have a smaller, more compact shape in wave-exposed than wave-protected habitats. However, the long, flexible kelps and large strong corals provide exceptions to this generality.

Some organisms form dense aggregations and this can help buffer then from the velocities and subsequent forces exerted by waves. Mussels, algae, and other organisms can often be limited in rocky substratum for attachment space. As a result, patches of densely aggregated individuals often form on suitable surfaces on wave-swept shores (**Figure 5**). Water motion caught inside aggregations can be damped and slowed. As hydrodynamic forces are proportional to water velocity, this can lead to reduced forces inside aggregations, as interior individuals may be buffered from fast water velocities by neighbors.

The Benefits of Life in a Wave-Swept Environment

Because waves can be so destructive, scientists have devoted a great deal of attention to understanding the strategies that organisms have evolved to avoid or cope

Figure 5 *Turbinaria* aggregation. Photo courtesy of Hannah Stewart.

with damage. However, not all of the ecological consequences of waves are negative. The vast numbers and diversity of organisms living in wave-swept environments indicate that the tradeoffs required for survival there are worthwhile. Many aspects of biological processes are enhanced by wave action.

Reproduction and Fertilization Success

Waves can have significant effects on the numbers of young organisms that produce and release into a population. Beneath breaking waves, the tumultuous water motion is characterized by high turbulence. This turbulence can have important effects on the success of fertilization, and therefore the number of young produced in broadcast-spawning species. Sexual reproduction via the release of sperm into the water column is widespread among marine organisms. Given the limited swimming capabilities of sperm, if adults are separated by more than a few centimeters, some water motion is required to bring sperm and eggs together. Turbulent mixing due to wave energy can be advantageous to bring gametes into contact; however, turbulence will also influence the dilution rate of the gametes and imposes viscous forces on them. If these forces inhibit the attachment of sperm to eggs or damage the gametes or zygote, the advantages of mixing can be negated. Thus, turbulent water motion can either aid or hinder fertilization depending upon the species and the degree of turbulence.

Dispersal of Young

The vast majority of marine benthic animals have a planktonic larval stage, and the dispersal and settlement patterns of these larvae are important determinants of population dynamics. Larval transport is greatly affected by the near-shore flow regime. In this case, a wave phenomenon known as ‘internal waves’ plays a role. Internal waves are similar to surface waves in being periodic undulations of a fluid interface, but internal waves happen within the ocean, at points where there are sharp gradients in the temperature or salinity of water. Such gradients often occur somewhere in the top 30 m of the ocean. Although internal waves cannot be seen by eye, they can be observed with thermometers mounted in the ocean. Though not as obvious as surface swell, internal waves have important ecological consequences. For example, tidally generated internal waves are accompanied by circulating cells of water near the surface, and on many shores these cells are advected shoreward with the internal waves. Larvae that can swim fast enough or are sufficiently buoyant to stay at the water’s surface are concentrated in areas of downwelling between cells and are consequently carried inshore. Internal waves thus provide a mechanism for returning dispersed larvae to the shore where they can settle and recruit into the population. The mass transports and long-shore and rip currents accompanying surface gravity waves provide alternative mechanisms by which larvae can be transported, in this case both on- and offshore. For any of these advective mechanisms, behavioral control by the larva over its position in the water column can affect the direction and rate of transport. Aside from advective transport, the process of turbulent mixing, common to wave-swept shores, may also disperse larvae.

Dispersal of Chemical Cues

Waves provide water motion that can spread settlement cues in the water column, but the back-and-forth motion of water in waves slows the rate at which chemical cues are advected away from their area of origin. As the cue moves in the oscillatory flow of waves, it becomes mixed with the surrounding water. Larvae of a coral-eating nudibranch have a settlement mechanism that takes advantage of this situation. When a larva experiences a settlement cue above a certain concentration, it stops swimming and sinks. Due to the oscillatory nature of water under waves, as the larva sinks it is moved back and forth but lands on the bottom roughly below the position in the water column where it sensed the cue. In this way, the simple behavior of the nudibranch and the water motion of waves provide a mechanism that increases the chances of a larva reaching its desired settlement site in a wavy environment.

Feeding and Nutrient Uptake

Turbulence in the benthic boundary layer is generated by the interaction of flow with the roughness of the substratum and can be augmented by mainstream turbulence from breaking waves. The intensity of this turbulence controls the rate at which suspended food and dissolved nutrients can be delivered to benthic organisms. If turbulent mixing is not sufficiently energetic, food or nutrients may become a limiting commodity. This effect has been demonstrated for populations of mussels in estuaries and for kelps in slow-moving flows. Nutrient limitation in kelps due to insufficient mixing appears to be a problem only at very low velocities.

Ecological Consequences

Disturbance and Patch Dynamics

Probably the most important and well-studied ecological effect of wave action is the effect of wave-induced disturbance to the community. Storms and intense wave action can be a leading agent of disturbance in marine

Figure 6 Patches created in an intertidal mussel bed by wave disturbance. Photo by Carol Blanchette.

communities. Disturbance plays a central role in nonequilibrium theories of community structure, including the concepts of disturbance theory, patch dynamics, and supply-side ecology. These theories attribute high species diversity and species coexistence to the processes of stochastic recruitment in a heterogeneously disturbed, patchy environment. The 'intermediate disturbance hypothesis' proposes that species diversity is highest in communities that are subject to moderate levels of disturbance. Disturbances have been shown to be important in many marine systems. For example, the rate at which waves clear gaps in intertidal mussel beds of the northeast Pacific creates opportunities for other, less competitive, species to settle and grow (Figure 6). Species diversity has been shown to be highest in intertidal boulder fields containing boulders of medium size, which are overturned more frequently than large boulders and less frequently than small boulders. Similarly, the rate at which storm waves cause breakage can have a controlling influence on the structure of coral reef communities.

Productivity

Intertidal organisms cannot transform wave energy into chemical energy, as photosynthetic plants transform solar energy, nor can intertidal organisms 'harness' wave energy. Nonetheless, example after example finds that communities exposed to high wave action are more productive than similar communities in less wave-exposed areas. Despite severe mortality from wave-driven storms, communities at some wave-beaten sites produce an extraordinary quantity of biological structures per unit area of shore per year. Highly productive organisms such as the sea palm, *Postelsia palmaeformis*, are restricted to wave-beaten sites. Water motion is known to enhance the growth of aquatic organisms. In general, productivity of marine and freshwater plants is higher in moving than in still water, and it has long been known that coral reef growth is most vigorous on those margins of the reef where waves pound hardest. Wave-beaten reef platforms produce four times as much calcium carbonate per square meter per year as do those in protected lagoons. Increased exposure to waves does not always increase productivity. Along the southern coast of Chile, the subtidal kelp *Macrocystis* appears to grow best at intermediate levels of water motion: at the most exposed sites, storm waves tear these kelps away. In the northeastern Pacific, however, intertidal kelps do grow better in wave-beaten places, even though waves select stringently for small size, because winter storms shred the fronds of most kelps, and tear away many kelps and mussels. In general, intertidal zones of the northeastern Pacific are more completely covered by plants and animals the more exposed they are to wave action. The mechanisms for this enhanced productivity are complex and different for different systems. However, the phenomenon is well documented as an important component of how waves influence intertidal communities.

Climate Change and Wave Activity

Will the changing climate of the future be accompanied by changes in the wave climate? Recent investigation has shown wave and storm activity to be highly correlated with the intensity of El Niño-Southern Oscillation events. Although it is unclear what mechanism could account for this relationship, the presence of such a correlation suggests that local wave exposure can be strongly affected by the type of large-scale climate phenomena that are currently the subject of intense predictive efforts. Researchers have also noted an increase in wind stress averaged over large areas of the sea surface for the seas adjoining California, Peru, Morocco, and the Iberian Peninsula. Wind stress is a large contributing factor in the formation of waves. These studies suggest that substantial fluctuations in the severity of the wave climate may be a common phenomenon. The ability to predict ecological effects of waves on species distributions will become increasingly important in the face of climate change. For example, many intertidal species present on the central California coast are at or near the limits of their biogeographic ranges. A shift in the rate of disturbance that results in even a slight shift in the ability of a given species to persist may in this case result in a substantial shift in that species distribution. Thus, the ability to make accurate mechanistic predictions regarding wave-induced disturbance may augment our ability to predict future shifts in species distributions.

See also: Ecosystem Patterns and Processes; Wind Effects.

Further Reading

Bascom W (1979) *Waves and Beaches*. Garden City, NY: Anchor Press.
Denny MW (1987) Life in the maelstrom: The biomechanics of wave-swept rocky shores. *Trends in Ecology and Evolution* 2: 61–66.
Denny MW (1988) *Biology and the Mechanics of the Wave-Swept Environment*. Princeton, NJ: Princeton University Press.
Denny MW (1995) Predicting physical disturbance: Mechanistic approaches to the study of survivorship on wave-swept shores. *Ecological Monographs* 65: 371–418.
Denny MW and Blanchette CA (2000) Hydrodynamics, shall shape, behavior, and survivorship in the owl limpet, *Lottia gigantea*. *Journal of Experimental Biology* 203: 2623–2639.
Denny MW, Daniel T, and Koehl MAR (1985) Mechanical limits to size in wave-swept organisms. *Ecological Monographs* 55: 69–102.
Hadfield MG and Koehl MAR (2004) Rapid behavioral responses of an invertebrate larva to dissolved settlement cue. *Biological Bulletin* 207: 28–43.
Kampion D (1989) *The Book of Waves*. Niwot: Roberts Rinehart Publishing.
Koehl MAR (1982) The interaction of moving water and sessile organisms. *Scientific American* 247: 124–132.
Koehl MAR (1984) How do benthic organisms withstand moving water? *American Zoologist* 24: 57–70.
Koehl MAR and Wertheim AR (2006) *Wave-Swept Shore, the Rigors of Life on a Rocky Coast*. Berkley: University of California Press.
Pedlosky J (2003) *Waves in the Ocean and Atmosphere: Introduction to Wave Dynamics*. Berlin: Springer.
Stewart HL (2006) Hydrodynamic consequences of flexural stiffness and buoyancy for seaweeds: A study using physical models. *Journal of Experimental Biology* 209: 2170–2181.
Vogel S (1996) *Life in Moving Fluids*. Princeton, NJ: Princeton University Press.

Weathering

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Introduction

The idea of cyclic processes in geology was very important for the development of scientific thinking. The eighteenth century was a time of rationalism and discovery. The Neptunists developed the idea that in the early stages of its evolution the Earth was covered by a universal ocean and the present continents have emerged by secular lowering of the sea level. A famous Neptunist was A. G. Werner according to whom the Earth's crust has been laid down as a series of worldwide formations by primeval ocean. Thus, the face of the Earth had been built and shaped mainly by the agency of water. In the opinion of the Plutonists, rocks were mainly the results of cycling of material derived from erosion of older rocks. According to J. Hutton the products of erosion accumulated on the seafloor where they became hardened by the Earth's internal heat. In this way, the Neptunist–Plutonist controversy of the eighteenth century already covered two general features of scientific thinking, the repetitious cycling of planetary matter on the one side and the directional evolution of the Earth on the other side. V. Vernadsky was the first who created the concept of biogeochemistry as the intersection of biological, geological, and chemical processes with the cycling of elements through the biosphere as the central process.

In this article, we discuss the importance of weathering in the framework of global geochemical cycling. After reviewing the global volatile cycle and the weathering process, we present a global carbon cycle model that includes both silicate and carbonate weathering. Furthermore, we describe in detail the biotic enhancement of weathering and the importance of weathering after heavy impacts.

Parametrized Convection Model with Volatile Exchange

The global volatile cycle is based on the interaction of the Earth's mantle and the surface reservoirs of volatiles. The transport of volatiles to and from the mantle is via mantle convection that can be described by parametrized convection models. Parametrized convection models have been developed for more than 30 years. They are applied to study the temporal variations of quantities such as average mantle temperature and heat flow by parametrizing the heat flow in terms of the Rayleigh number Ra:

$$N \propto Ra^{\beta} \qquad [1]$$

where N is the ratio of the total heat flow and the conductive transported heat (Nusselt number) and β is an empirical constant, usually equal to 0.3.

The effect of volatile-dependent rheology on the thermal evolution of the Earth was first analyzed by showing that the existence of volatiles has a significant effect on the thermal history of the mantle.