

# Chapter 1

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## Ecological Mechanics *An Introduction*

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“The key to prediction and understanding lies in the elucidation of mechanisms underlying observed patterns.” (Levin 1992)

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**mech-an-ism**, *n.* **1.** an assembly of moving parts performing a complete functional motion, often being part of a large machine; linkage. **2.** the agency or means by which an effect is produced or a purpose is accomplished. (*Random House Dictionary of the English Language, Second Edition*)

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This is a book about the mechanisms of biology: an exploration of how organisms function as individuals, how they are linked to each other and to the physical environment, and how these linkages affect the dynamics of populations and ecological communities. What sets this text apart from most other ecological investigations is its emphasis on biomechanics, the branch of physiology that uses the principles and perspectives of physics and engineering to study plants and animals. When properly applied, a biomechanical approach to ecology can provide valuable information unattainable by more traditional means, information we need to understand how organisms, populations, and communities function. My intent in this text is to open your eyes to this new way of thinking. A brief example will give you a feeling for how this approach works and where this book is headed.

## 1 MECHANICS AND ECOLOGY COMBINED *Coral Reefs*

Foundation species (also known as ecosystem engineers) create or modify physical habitats, thereby influencing community structure and dynamics. Beavers are literal

engineers—they build dams, which can have important impacts on stream ecology. Trees in rain forests and giant seaweeds in kelp forests are other obvious examples of foundation species. But the poster children of ecosystem engineering are corals.

Tropical coral reefs are perhaps the largest biological construction projects on Earth, hosting a diversity of life that is among the highest on the planet (Figure 1.1A). However, these reefs exist in delicate balance. Corals and macroalgae (seaweeds) compete for light and space, and a small shift in environment or community dynamics could potentially turn the world's coral reefs into algal reefs (Knowlton and Jackson 2001).

Recently, the application of principles drawn from ecology, engineering, and fluid dynamics has produced a major advance in our understanding of how coral reefs interact with their physical environment. Working at Lizard Island (part of the Great Barrier Reef in Australia), Josh Madin and his colleagues used a biomechanical approach to link ocean climate and chemistry to reef diversity and species distributions.

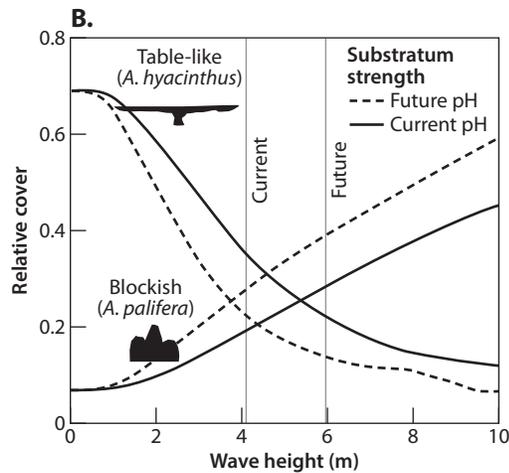
Much of the food available to corals comes from symbiotic microalgae in the coral polyps (not to be confused with the seaweeds that help to form reef structure). These microalgae need to absorb sunlight, which confines corals to shallow water where they are exposed to sufficient illumination, but also subjects them to rapid water velocities as waves pass overhead. The goal of Madin's research was threefold:

- first, to quantify the mechanisms by which this flow environment controls the relative abundance of coral species,
- then, to develop a model using those mechanisms to explain the observed spatial pattern of coral species on the reef,
- and finally, to use that model to predict how reef community dynamics will shift in response to climate change.

First, the mechanics. The ability of a coral colony to survive the hydrodynamic forces imposed by waves depends on several factors: the strength of both the colony's skeleton and the substratum, the size and shape of the colony, and the maximum water velocity encountered. Madin (2005) began his investigation of these factors by quantifying the mechanical attributes of the corals. He collected samples of coral skeleton and the substratum to which they were anchored, and by pulling on them with a materials testing machine he measured the strength of each. He then used beam theory (a branch of engineering) to calculate how much hydrodynamic force it would take to dislodge coral colonies of different sizes and shapes. He found that the strength of the substratum was the limiting factor, and that tablelike corals such as *Acropora hyacinthus*, which have relatively small bases, break under smaller loads than do blocky corals such as *Acropora palifera*.

The next step was to estimate the minimum water velocity necessary to impose these breaking forces. This was accomplished using a well-known result from fluid dynamics: force is proportional to the area of coral exposed to flow and to the square of water velocity.

At this point, all that Madin needed to predict which species would be living where on the reef was a record of the water velocities corals had experienced while growing to their present size. It would have been handy if someone had recorded velocities on the reef for the decades it took the corals to mature, but records of this sort are exceedingly rare, and none were available for Lizard Island. Instead, Madin et al. (2006) used their knowledge of physical oceanography to gather the required data.



**Figure 1.1 A.** Coral reefs are home to an extraordinary diversity of life forms ([www.noaa.gov/features/climate/images/fig1\\_reef\\_fullsize.jpg](http://www.noaa.gov/features/climate/images/fig1_reef_fullsize.jpg)). **B.** Relative cover of species changes with wave height and ocean pH. Currently, tablelike *Acropora hyacinthus* is more abundant than blockish *A. palifera*, but a reduction in pH or an increase in wave height could reverse the order. Redrawn from J. S. Madin, M. J. O'Donnell, and S. R. Connolly. 2008. "Climate mediated changes to post-disturbance coral assemblages." *Biol. Lett.* 4:490–93, by permission of the Royal Society.

They first obtained a 37-year record of wind speeds near Lizard Island (unlike records of water velocity, wind-speed records are common) and used the theory of wave generation to translate the wind's history into a 37-y record of wave heights. To check the accuracy of their results, they videotaped waves during known wind speeds and found that the theory was remarkably accurate.

They then used wave mechanics (a branch of fluid dynamics) to predict how wave height evolves as waves move onto the reef and what velocities would consequently be imposed on corals. The net result was a 37-y record—a hindcast—of the flow experienced by corals at every point in the habitat. Again, they checked their results with measurements made on the reef.

With these data in the bag, Madin and Connolly (2006) had the raw ingredients for a mathematical model of the life and death of corals. Knowing how water velocity varied through time at every point on the reef, they could predict how big each of the 1158 colonies they studied could grow without being broken. Their predicted size limits matched those observed on the reef, suggesting that their model of coral survival—from wind to waves to the mechanics of individual coral heads—was a valid description of reality. Unlike previous work, which had noted *correlations* between water motion and coral size (e.g., Done 1983), Madin and Connolly's model provided a mechanistic, quantitative *explanation* of the observed distribution.

Madin et al. (2008) then looked to the future and asked how climate change might affect the reef. In particular, they focused on two aspects of the environment that are likely to shift dramatically in the next few decades. First, climate models predict that the frequency and intensity of typhoons will increase at Lizard Island (Elsner et al. 2008; Young et al. 2011), leading to an increase in the forces imposed on corals. Second, due to the absorption of carbon dioxide by seawater, ocean acidity is predicted to intensify on the Great Barrier Reef (Kleypas et al. 1999, Hoegh-Guldberg et al. 2007), resulting in a decrease in the strength of the reef's carbonate substratum. Considering these effects in tandem, Madin et al. (2008) predicted that if, in a more acidic future ocean, a typhoon produces waves 6 m high (compared to the average maximum of 4.2 m over the 37 y of their hindcast), the fraction of space occupied by tablelike species will drastically decrease (from almost 40% to near 10%), while the abundance of blockish colonies will increase (Figure 1.1B). Note that the shift in species abundance is amplified by the interaction of waves and acidity: each factor on its own would have less drastic consequences.

This model and its predictions are an important advance in coral-reef ecology because they provide a robust basis for predicting the consequences of climate change—not just for corals, but for the whole reef community. For instance, the density of herbivorous fish on reefs is tied to the abundance of branching and tablelike corals, the fishes' preferred habitat (Luckhurst and Luckhurst 1978; Knowlton and Jackson 2001; Almany 2004). The predicted decrease in cover of these delicate corals at Lizard Island may, therefore, cause a decrease in herbivory, shifting the interaction between corals and macroalgae (Mumby 2006) and potentially pushing the reef to the point where seaweeds dominate.

Madin's studies convey the spirit of this text's approach. Without a thorough understanding of the mechanisms linking wind to waves to force and ultimately to breakage and climate change, it would be impossible to accurately model the dynamics of coral species' distribution. Similarly, without ecologists' understanding of fish behavior and natural history, it would be impossible to extrapolate from information regarding species distributions to predict the ensuing effects of climate change on

community dynamics. Individually, biomechanical and ecological approaches are incomplete, but working together they provide valuable tools for predicting the future.

## 2 RESPONSE FUNCTIONS

As illustrated by this example, my strategy in this text is to explore *response functions*, the relationships between the conditions imposed on a system and how well the system performs. More specifically, response functions are mathematical descriptions of the cause-and-effect linkages between an input variable (such as wave height) and an output variable (such as hydrodynamic force). *Measured response functions* describe existing data without reference to underlying mechanism; *mechanistic response functions* use established principles of physics, physiology, and behavior to model reality. Mechanistic response functions have two important advantages: they allow for accurate extrapolation beyond measured data, and we can judge their validity by comparing their predictions to empirical observations.

An example again helps to explain what I mean. Inspired by Madin's work, a researcher might propose to study the dynamics of sea urchins foraging on seaweeds. At the study site, when hydrodynamic forces are small, urchins are free to roam, and their foraging can decimate the local seaweeds. By contrast, if forces are sufficient, urchins are dislodged or confined to their burrows, and seaweeds can flourish. As a first step toward investigating this process, our researcher might use a flow meter to measure the relationship between wave height and the ensuing hydrodynamic forces imposed on urchins (the dots in Figure 1.2A). Note that for practical reasons the researcher is able to make measurements only when wave conditions are relatively benign. This relationship is a measured (empirical) response function.

Phenomenological descriptions of this sort are valuable, but my desire in this text is to take the next step: to investigate not only what happens, but also *why* it happens. Knowing why can be important. For instance, if our researcher were naively to extrapolate from the empirical information in hand (Figure 1.2A), he or she would predict that waves of a height encountered in storms could impose forces on urchins large enough to disrupt their feeding. According to this prediction, any future increase in ocean storminess would increasingly restrict urchin foraging and favor seaweed dominance.

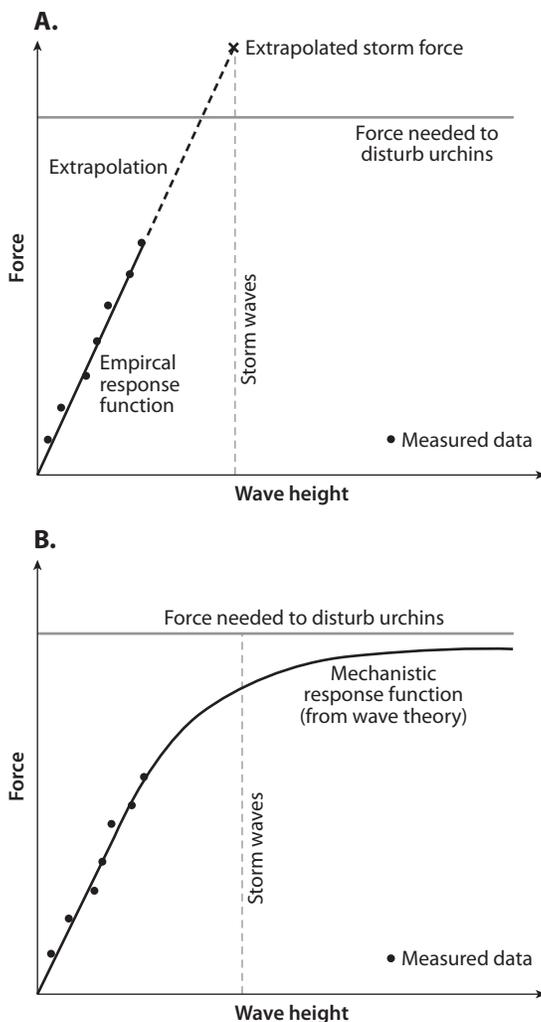
However, before relying on this extrapolation and its ecological implications, it would be wise for our researcher to investigate the fluid dynamics of waves to understand the mechanism behind his or her measurements. In this case, theory would reveal that, at the relatively low wave heights of the measured data, waves are intact as they pass over the urchins, and force should indeed increase in direct proportion to wave height. This match between theory and measurement serves as a check that the theory is correct. But theory also predicts a limit to this linear relationship—in the relatively shallow water of the field site, high waves become unstable and break before reaching the urchins, dissipating much of their energy and reducing their height (Helmuth and Denny 2003). This understanding of mechanism—the *why* of the process—allows the researcher to formulate a mechanistic response function, one that predicts that force will plateau before reaching levels that would bother urchins (Figure 1.2B). Because it is based on mechanics in addition to observations, this response function provides increased accuracy when extrapolating beyond the measured data. In this case, the researcher would predict that increasing storm

**Figure 1.2 A.** An empirical response function (solid line) fits the measured data (the dots), and a linear extrapolation suggests that storm waves will dislodge urchins. **B.** By contrast, a mechanistic response function also fits the data, but its more accurate extrapolation suggests that urchins can weather the storms.

intensity would have negligible effect on urchin grazing. As a result, he or she should propose that, even if the ocean gets wavier, seaweed abundance won't increase.

Response functions (both measured and mechanistic) are commonplace in many fields of biology. Biomechanics (the field in which I was raised) revels in its ability to use Newtonian physics—an extraordinarily useful set of response functions—to explain how individual plants and animals work. Ecological physiology investigates the functional relationships between individual organisms and the physical environment. And in ecology, response functions are used to specify, for instance, the rate of prey capture as a function of prey density.

Despite the ubiquity of response functions, biologists are seldom taught how to recognize, classify, and use them. It doesn't help that different fields use different synonyms for what I call response functions. In physiology, for instance, measured response functions are commonly referred to as reaction norms. In ecology, predator-prey response functions are known as the functional response. In physics and engineering, some mechanistic response functions are so well established they are called laws. This text is intended, in part, to push through the barriers of jargon. By raising the awareness of response functions in general, I hope to impress on you how the basic concepts of response functions can unify different perspectives on biology, and to demonstrate that an understanding of mechanistic response functions can be used to great advantage in ecology.



### 3 TRANSPORT PHENOMENA

Many of the response functions we will encounter in this text involve transport phenomena, the movement of heat, mass, and momentum. Consider, for example, body

temperature in the sea star, *Pisaster ochraceus*. *Pisaster* is the principle predator of mussels on the west coast of North America, acting as a keystone species (Paine 1966). As *Pisaster* consumes mussels (the dominant competitor for space on rocky shores), it opens up space for less capable competitors, thereby increasing species diversity. But, the rate at which *Pisaster* feeds depends on its body temperature. An increase of only 4°C (from 9.5°C to 13.5°C) doubles the rate at which *Pisaster* consumes mussels (Sanford 2002), so even a slight increase in temperature could have a substantial effect on mussel-bed community structure.

Engineering theory (which we will explore in Chapters 11 and 12) tells us that *Pisaster*'s body temperature depends on the rate at which heat is transported into the animal (from the absorption of sunlight, for instance) relative to the rate at which it is transported out (by evaporation, convection, or conduction). Thus, if we desire to predict *Pisaster*'s body temperature—and, thereby, its effect on community dynamics—we would be well advised to begin by studying the transport of heat.

Similar advice applies to the transport of mass. A plant's growth rate often depends on the rate at which it can acquire carbon dioxide and nutrients, forms of mass that must be transported to the organism. As we will see, transport of mass depends on the pattern of flow adjacent to a plant—laminar or turbulent—and that pattern depends on the speed of the medium—water or air—and the shape and size of the plant. Thus, if we want to predict the growth rate of a kelp or cactus, we need to understand how fluid flow governs the transport of mass.

The relevance of momentum transport is perhaps less immediately obvious, but we will find in Chapter 2 that the application of a force requires the transfer of momentum. When waves impose hydrodynamic forces on corals, for example, they do so because some of the moving fluid's momentum is, in effect, absorbed by the animals. Indeed, the transport of momentum is an underlying theme in all Newtonian mechanics.

Clearly it is valuable to understand the transport of heat, mass, and momentum, and each process is important as a separate phenomenon. But engineers have developed a theoretical perspective that can compound their utility. Because the movements of heat, mass, and momentum are all transport phenomena, knowledge about one can inform the others. For example, we will see in Chapter 11 that it is easy to measure the rate at which heat is transported out of a plant or animal by flowing fluid—in a nutshell, you heat the organism and measure how quickly it cools. By contrast, it can be much more difficult to directly measure the rate at which mass is transported to or from the same organism. For instance, the ability of a male moth to find a mate depends on the delivery of picograms of pheromone to its antennae. Directly measuring the delivery of such minuscule mass would be extremely difficult. But because the mechanism of mass transfer is similar to that of heat, information about the flow of heat from the antennae—which is relatively easy to obtain—can be used to estimate the rate of mass exchange. Similarly, measurements of the temperature of a leaf can be used to estimate the rate at which it takes up carbon dioxide and loses water.

In short, by recognizing that fluxes of heat, mass, and momentum are all transport phenomena, we set the stage for an extraordinarily productive synthesis of ideas.

## 4 WHAT'S IN A NAME?

The preceding discussion outlines the perspective of this text—with the goal of informing ecology, we will use response functions (mechanistic where possible,

measured when necessary) to explain how plants and animals work and interact. To streamline the prose, we need a name for this approach. Several possibilities come to mind. None is entirely satisfactory, but the phrase *ecological mechanics*—*ecomechanics* for short—seems to be the best of the lot,<sup>1</sup> and the term has a distinguished heritage; it was first used by Wainwright et al. (1976) in their classic treatise on mechanical design in organisms. Taoist philosophy warns, however: “all that is dark derives from the labeling of things” (Mitchell 1998), so it is best if I clarify my intent in choosing this label.

By using ecomechanics to describe this text’s perspective, I do not mean to imply that this approach is absent from current-day research. As noted previously, mechanistic approaches are in fact widely used: functional ecology, biophysical ecology, bioenergetics, ecological physiology, biomechanics, and materials science (among others) all view the study of biological mechanisms as their central modus operandi in much the fashion I propose here.

In each case, however, the focus and range of these mechanistic approaches are restricted compared to my vision for ecomechanics. Biomechanics and functional ecology, for instance, have historically concentrated their efforts at the level of the organism rather than extending their mechanistic approach to higher levels of organization. Biophysical ecology and bioenergetics emphasize the transfer of heat and mass between organisms and their environment but de-emphasize the role of momentum transfer, that is, of forces. Ecological physiology focuses on the processes through which organisms survive but, other than at the cellular level, generally neglects the structures and materials that make those processes possible. And materials scientists seldom consider the physiological and ecological implications of their findings.

In proposing the term ecomechanics, my intent is to emphasize the commonality of research philosophy that unites these fields. I hope that this text will foster cooperation among disciplines and across levels of organization, from molecules to ecosystems.

## 5 WHAT’S LEFT OUT

To keep this text from becoming unwieldy, I have had to make tough choices as to what to include and what to leave out. Two criteria guided these decisions. First, the emphasis here is on the physical interactions among organisms and between organisms and their environment. Consequently, even though they clearly fall within ecomechanics’ purview, those aspects of physiology that deal with organisms’ internal working receive short shrift. Second, I have minimized discussion of ecomechanical

<sup>1</sup> To some, mechanics is narrowly defined as the study of forces and the motions they cause. Because the purview of ecological mechanics, as described here, includes many aspects of biology that do not involve forces, inclusion of the term *mechanics* is thus deemed inappropriate. However, this definition of mechanics is unnecessarily narrow. For example, the *Random House Dictionary* defines mechanics as the “branch of physics that deals with the action of forces on bodies and with motion, comprised of kinetics, statics, and kinematics.” The phrasing of this definition and the inclusion of kinematics (the study of motion without regard to forces) implies that force is not essential to mechanics. As long as one takes an inclusive view of things in motion (e.g., heat, mass, momentum, energy, information), the appearance of mechanics in ecological mechanics and ecomechanics should cause no more of a problem than it does in the term quantum mechanics.

topics that are well covered in other texts. In particular, I have omitted coverage of sound and hearing (whose physics are explained by Fletcher, 1992) and light and optics (well explained by Johnsen, 2012) and have included only a brief overview of low-Reynolds-number fluid dynamics, a topic admirably covered by Kiørboe (2008) and Dusenbery (2009). As partial compensation for the remaining omissions, I have included in the appropriate sections directions to useful sources of information on the many worthy topics I have been forced to exclude.

## 6 A ROAD MAP

Our exploration of ecological mechanics is divided into four parts. This chapter and the two that follow (Part I) set the stage by providing an introduction to the ecomechanical perspective, basic principles of Newtonian physics, and the concept of response functions.

Part II develops the theme of heat, mass, and momentum transport, with chapters on diffusion, fluid mechanics, boundary layers, hydrodynamic forces, locomotion, and thermal biology.

Next, Part III deals with the structural response of organisms to the forces imposed on them—how organisms bend, twist, and break.

Lastly Part IV synthesizes information from the previous sections in an ecological context. We examine the role of variation in response functions, and how variation depends on the scale of measurement. We delve into the statistics of extremes, and explore how mechanistic response functions can be used to predict the patterns in which organisms assemble.

## 7 ONLINE SUPPLEMENTS

In my quest to keep the message simple, I have been forced to leave out many of the intriguing (but complex) details and all but a few of the derivations of equations. Fortunately, the Internet provides a means for those details and derivations to be available to the interested reader. Throughout the text, I note where further discussion of a topic can be found in an online supplement. (Supplements—along with problem sets, additions, and corrections—can be accessed through the book's Web page within the Princeton University Press site, <http://press.princeton.edu/titles/10641.html>.) Some of these supplements are quite short—the proof of an assertion or a brief anecdote—but others are extensive, amounting to whole chapters on subjects that could not be included in the text. I have also included problem sets so that you can test your understanding.

## 8 A NOTE ON NOTATION

In a subject this broad, finding unique symbols for variables is well nigh impossible. Due to the limited number of Greek and Roman letters, I have been forced to use some symbols more than once, but I have endeavored to minimize the repetition. To help you keep symbols straight, there is an index to the page where each is defined. The letter  $k$  is a special case—I employ it as utility variable, defined in the context of each local discussion. So be warned, unlike other symbols,  $k$ 's identity changes frequently.

Now, on with the show.