

# Marine Ecomechanics

Mark W. Denny<sup>1</sup> and Brian Gaylord<sup>2</sup>

<sup>1</sup>Hopkins Marine Station, Stanford University, Pacific Grove, California 93950; email: mwdenny@stanford.edu

<sup>2</sup>Bodega Marine Laboratory and Department of Evolution and Ecology, University of California, Davis, Bodega Bay, California 94923; email: bpgaylord@ucdavis.edu

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## Key Words

dispersal, disturbance, coral reefs, mussels, fertilization ecology, kelps

## Abstract

The emerging field of marine ecomechanics provides an explicit physical framework for exploring interactions among marine organisms and between these organisms and their environments. It exhibits particular utility through its construction of predictive, mechanistic models, a number of which address responses to changing climatic conditions. Examples include predictions of (*a*) the change in relative abundance of corals as a function of colony morphology, ocean acidity, and storm intensity; (*b*) the rate of disturbance and patch formation in beds of mussels, a competitive dominant on many intertidal shores; (*c*) the dispersal and recruitment patterns of giant kelps, an important nearshore foundation species; (*d*) the effects of turbulence on external fertilization, a widespread method of reproduction in the sea; and (*e*) the long-term incidence of extreme ecological events. These diverse examples emphasize the breadth of marine ecomechanics. Indeed, its principles can be applied to any ecological system.

## INTRODUCTION

Ecology—the study of relationships among organisms, and between organisms and their environments—often focuses on patterns of distribution and abundance. Prompted in part by anthropogenic climate change, ecologists have recently renewed their emphasis on the ways in which organisms interface with the physics of their surroundings. Perhaps nowhere in ecology is this truer than in marine systems where characteristics of the fluid medium play paramount roles at scales from molecular to global.

The field of marine ecomechanics focuses on these physical interactions and draws them to the fore. Originating from a recognition that essentially all arenas of marine ecology are influenced by environmental physics, ecomechanics' goal is to explicitly connect the analysis of physical principles; the responses of organisms to physical factors; and the resulting consequences for the form, function, and population pattern of organisms. An implicit—and equally important—intent is to develop these elements into a framework that provides quantitative predictive power.

Rationale for the ecomechanical perspective can be found in some of the fundamental tenets of marine ecology. For example, local species diversity is often explained using the intermediate disturbance hypothesis, and in Connell's (1978) classic treatment of the subject, wave action is a primary disturbing agent. In this instance, mechanics (fluid dynamics and the strength of materials) affects the death rate of individuals. In other cases, birth rate is an equally important driver of interest. Metapopulation theory, for example, relies on quantification of the colonization (i.e., birth) rate of subpopulations, a function of population connectivity (Levins 1969, Hanski 1999). For marine species, connectivity is often controlled by dispersal of microscopic larvae or spores, and hydrodynamic and oceanographic transport mechanisms become intrinsic concerns. Analogous relationships often underlie linkages between physics and reproduction more generally. Broadcast spawners release gametes into the water column, where fluid movement (including turbulent mixing) influences fertilization success and thereby the entry of new individuals into populations. Agents of density-independent population control, many of which occur as sporadic, extreme events (e.g., temperature maxima), provide additional examples where physical-biological interactions matter. Ecomechanics aims at a physically based understanding of these interactions.

What distinguishes marine ecomechanics from related fields of marine biomechanics, physiological ecology, and functional ecology? It is impossible to define distinct boundaries between fields such as these that are inherently so interdisciplinary, but it is nonetheless possible to place marine ecomechanics in context. Our view, admittedly one based as much on gestalt as objective analysis, is that biomechanics typically focuses on how individual organisms cope with or exploit their physical environments. Form and function are the subjects of prime concern, whereas ecological concepts and issues—particularly those that operate at the population level—receive less attention. Physiological ecology and functional ecology fall closer in aim to ecomechanics, but do not always emphasize as deep a level of physical dissection. Marine ecomechanics therefore differs from these other fields in the degree to which it extends beyond the individual to focus on population, community, and ecosystem ramifications, and in the degree to which it prioritizes physically based, quantitative prediction. Here we review a select set of five examples where explicit attention to physical-biological linkages—in some cases linkages operating across vastly different scales—informs organismal and ecological pattern and facilitates our ability to anticipate consequences of ongoing and future changes in the environment. Our intent is not to provide an encyclopedic review of marine ecomechanical studies (length constraints necessitate the exclusion of much excellent work), but rather to highlight the potential of this burgeoning field of inquiry.

## COMMUNITY STRUCTURE OF CORAL REEFS

Coral reefs, the iconic bioconstructs of tropical oceans, are under siege from a variety of stresses (Bellwood et al. 2004). Some have purely ecological causes, but others are due to ongoing shifts in the physical environment (Connell et al. 1997). The ecomechanical approach is now poised to make quantitative predictions of how coral-reef communities will respond to these future environmental changes.

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**Mechanical stress:**  
in a physically based,  
ecomechanics context,  
force per area

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### Hydrodynamics

Ocean waves are the primary drivers of water motion over coral reefs. For many ecomechanical purposes, simple linear wave theory is sufficient to provide accurate estimates of the flow field associated with waves of a given height and period acting at a given depth on a reef (e.g., Denny 1988, Massel 1996). As waves move shoreward into ever shallower water (a process known as shoaling), wave height increases, wavelength decreases, and the wave form steepens (see Denny 1988, Massel 1996). The increase in wave height leads to an increase in water velocity and acceleration at the substratum where corals live, but at some point—generally near the reef crest—steepening waves becomes unstable and break. Energy is subsequently lost to the viscous consequences of turbulence, and as waves reform behind the reef crest, their height and the resulting water motions are much reduced. This predictable spatial variation in flow (and the hydrodynamic forces that result) helps to determine where corals of a given size and shape can survive (Done 1983, Sousa 1984).

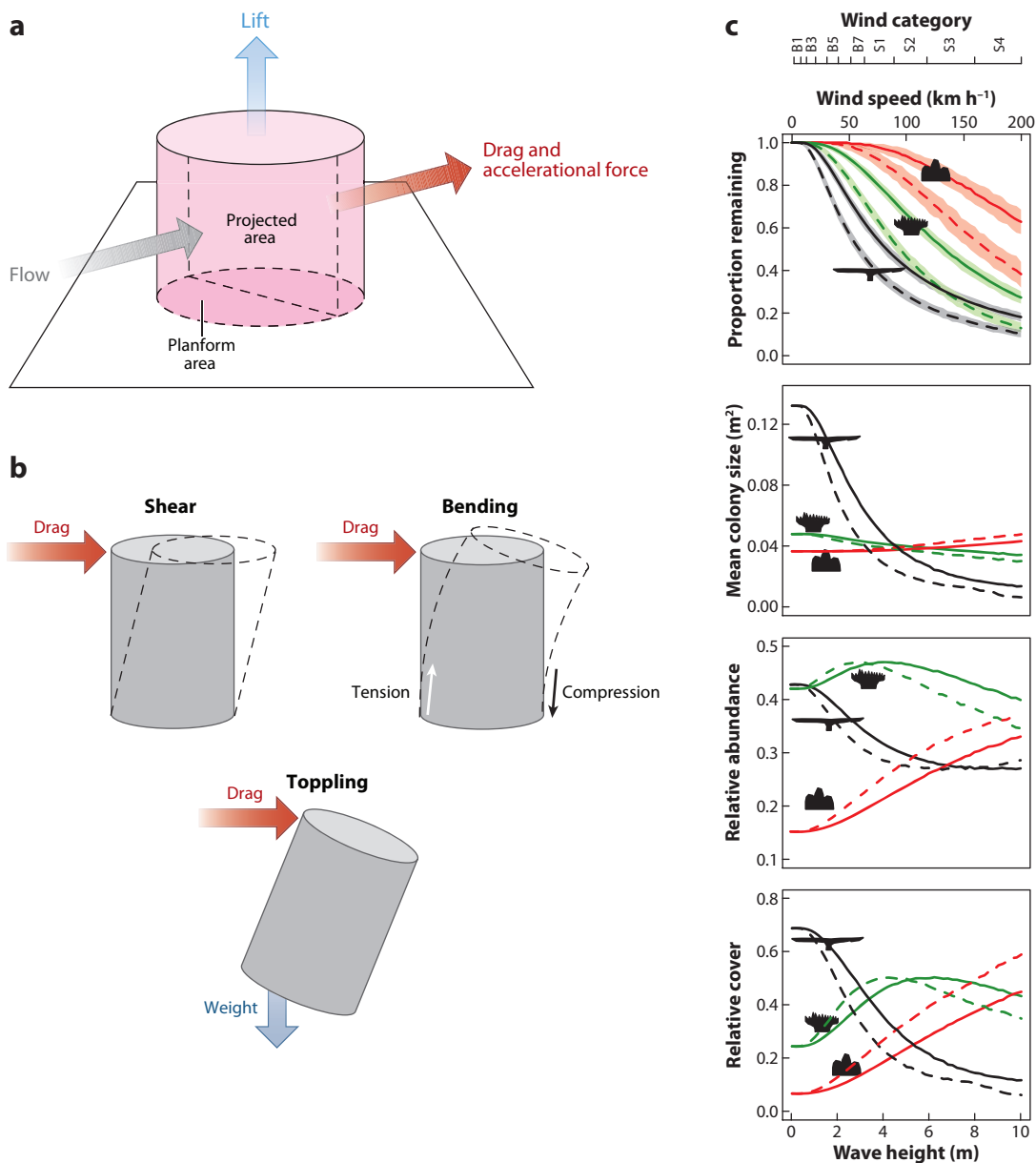
Wave-induced water motion causes three hydrodynamic forces (Denny 1988, Vogel 1994, Massel 1996). Drag pushes objects downstream with force proportional to the area projected in the direction of flow and to the square of water velocity (**Figure 1a**). Drag depends on the object's shape: A bluff body feels greater drag than does a streamlined shape of equal projected area. Lift acts much like drag except that it is directed perpendicular to flow, generally away from the substratum (Denny 1988). For lift, the pertinent area is an object's planform area, its area projected onto the substratum. The third force—the accelerational force—acts in the direction of water acceleration (generally parallel to velocity), and it differs from drag and lift in two important respects (Gaylord 2000): It is proportional to object volume rather than to projected area, and it is proportional to water acceleration rather than to velocity. Shape matters for the accelerational force, usually in a fashion similar to that for drag.

Which of these forces are important to corals depends on the size and shape of the coral colony. Small, branching corals have large projected areas relative to their volume, and for them, drag dominates (Madin 2005). Large, massive corals have small projected areas relative to their volumes, and for them, accelerational force is largest (Massel and Done 1993, Massel 1996). To date, no case has been found in which lift is an important component of force on corals.

Given information about the height and period of offshore waves, the pattern of shoaling, location of a colony on the reef, and the colony's size and shape, the hydrodynamic forces imposed on the colony can be calculated (Madin 2005). The challenge, then, is to predict the structural and ecological consequences of these forces.

### Mechanics of Corals

In response to the combination of drag and the accelerational force, a coral colony is pushed along the axis of flow and its skeleton is subjected to three mechanical stresses (**Figure 1b**). Shear stress tends to slide skeletal material relative to itself as one might skew a pack of cards, but beam theory



**Figure 1**

(a) When exposed to flow, an object is subjected to drag, lift, and accelerational forces. If velocity decreases through time, the accelerational force acts in a direction opposite of drag. (b) When subjected to drag, an object can shear, bend, or topple. (c) The relative abundance of massive coral colonies is predicted to increase if waves become higher in the future, while the abundance of tabular corals will decrease. Predictions are shown for three coral species surviving waves of a given height as they impinge on the reef at Lizard Island. Solid curves represent predictions based on current substratum strength; dashed curves represent predictions based on substratum strength halved by projected increases in ocean acidity. Symbols depict typical profiles for *Acropora hyacinthus* (squat "T" profile), *A. gemmifera* (spiky profile), and *Isopora palifera* (three-bumped profile). Adapted with permission from Madin et al. 2008.

(Denny 1988, Gaylord & Denny 1997, Madin 2005) tells us that shear stress is small compared with stress imposed by the tendency of hydrodynamic force to bend the colony. As it bends, the upstream side of the skeleton and the substratum to which it is attached are placed in tension and the downstream side is compressed. Coral skeleton is strong in compression but weak in tension (Madin 2005). As a result, the downstream compressive stress (like the shear stress) is easily resisted, but the upstream tensile stress can be problematic. In general, the most drastic effect of wave-induced hydrodynamic forces is to break the colony at the upstream end of either a branch or the colony's base (Madin 2005). Even when broken free from the substratum, massive coral colonies may be held in place by their weight, but they are susceptible to toppling (Massel & Done 1993). Empirical measurements of the size of a colony, the structural strength of a colony and its substratum, and the colony's shape allow prediction of a colony's mechanical fate for a variety of wave conditions at multiple locations on the reef.

## Predictions

The approach outlined above was first sketched by Massel & Done (1993) and has been applied to the reef at Lizard Island, part of the Great Barrier Reef in Australia. Because offshore ribbon and patch reefs protect Lizard Island from open-ocean swells, its reef is subjected only to waves aroused by local winds. As a result, Madin et al. (2006) could accurately hindcast the wave climate at Lizard Island from a 37-year record of winds. In conjunction with a detailed model of wave shoaling, they used this record to calculate maximum water velocity as a function of location relative to the reef crest. In another computational model, three coral species [*Acropora gemmifera*, *A. hyacinthus*, and *Isopora* (formerly *Acropora*) *palifera*] were placed in this flow environment, and hydrodynamic stresses were calculated (Madin & Connolly 2006, Madin et al. 2008). The predicted size and spatial distribution of surviving colonies in the model closely matched those in the field, providing mechanistic validation of the hypothesis that hydrodynamics plays a controlling role in coral distribution.

The ability to account for the existing distribution and abundance of corals on this reef is a milestone in marine ecomechanics, but the true value of the approach lies in its ability to predict the effects of climate change. Current climate models predict that typhoons in the Great Barrier Reef area will become more numerous and more intense as the planet warms (IPCC 2007), leading to larger waves impinging on Lizard Island. The 37-year wind history for Lizard Island included a moderate cyclone, allowing Madin et al. (2006) to calculate the corresponding flows and Madin et al. (2008) to predict how the relative abundances of their three species would respond to extreme wave events: The abundance of tabular *A. hyacinthus* would decrease relative to the other, more robust species (**Figure 1c**).

In addition to becoming possibly more wavy, the ocean is becoming more acidic. The increasing acidity of the ocean reduces the strength of the carbonate substratum to which corals are attached (Kleypas et al. 1999), reducing the height of waves necessary for dislodgment or overturning. The mechanical effects of these combined environmental stressors vary from species to species depending on coral colony morphology. Madin et al. (2008) predicted an accelerated change in species composition away from fast-growing branching corals to slower-growing massive corals (**Figure 1c**). This shift may have cascading consequences. For example, although they are more mechanically robust, massive corals provide less of the heterogeneous topographic habitat preferred by herbivorous reef fishes, and without sufficient herbivory, coral reefs are overgrown by algae (Knowlton & Jackson 2001).

Models of the type proposed by Madin et al. (2008) have great potential but are not yet complete. Refinements to the Madin model are needed to account for the ability of broken branches of some

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**Wave exposure:** the sum total of biological effects accruing from waves breaking on a shore

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species to reattach to the substratum and form new colonies (e.g., Smith & Hughes 1999). For these species, this mechanical fragmentation is the primary mode of reproduction and a key factor in their ability to dominate space (Tunnicliffe 1981, Highsmith 1982). The computation of wave shoaling and breaking used by Madin et al. (2008) will require refinement for application to specific sites on more topographically complex reefs. The growth rates of both corals and their algal competitors vary as a function of flow, and the models of Madin et al. (2008) should be expanded to include these effects. Lastly, although considerable effort has been expended studying coral skeleton as a source of information about paleoenvironments (reviewed by Barnes & Lough 1996), our understanding of coral skeletal mechanics is rudimentary. If we are to accurately predict the complex effects of rising temperatures, falling pH and carbonate saturation state, and altered storm activity, we need more detailed physiological and mechanical insight into the formation of coral skeletal material.

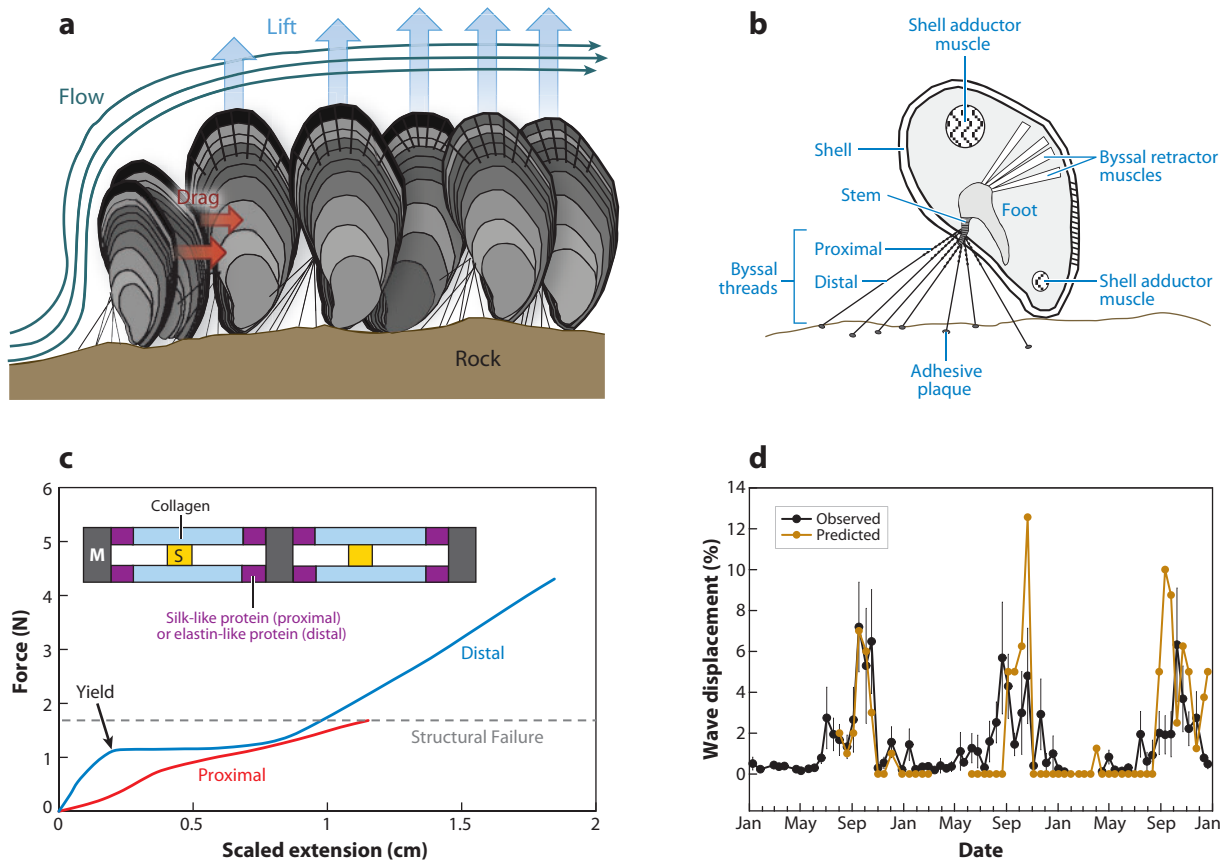
## DISTURBANCE OF MUSSEL BEDS

Mussels, like corals, are foundation species (*sensu* Dayton 1972). Their beds form a characteristic band in the mid-intertidal zone, physically excluding other occupiers of primary space while providing habitat for a diversity of infaunal organisms (Seed & Suchanek 1992). For mussel beds, the lower limit is typically controlled by the interaction between recruitment and sea-star predation and the upper limit by desiccation (Robles & Desharnais 2002), but within the bed itself, the ability of mussels to dominate space is limited primarily by the dislodgement of individuals by waves (Dayton 1971, Paine & Levin 1981). Dislodgment opens patches of bare substratum in the bed, temporarily providing space for fugitive species, but these “weeds” are eventually snuffed out by reincursion of the bed. In this fashion, the mussel-bed community responds dynamically to the tug-of-war between dislodgment and reestablishment. Thus, if we can predict the rate of mussel removal as a function of wave exposure, we can predict much about the spatial and temporal patterns of this model community and its response to environmental change.

Paine & Levin (1981) suggested that predicting mussel disturbance was “like predicting the weather,” implying that stochastic models are required to mimic the capricious complexity of the system. In the ensuing 28 years, our understanding of dislodgment mechanics has drastically increased, however, and mussels are now a prime example of the potential of marine ecomechanics’ to accurately predict the interaction between ecology and environment.

## Hydrodynamics

As waves crash on rocky intertidal shores, water velocities in excess of  $30 \text{ m s}^{-1}$  may be imposed on mussels (Denny et al. 2003), inducing potentially lethal hydrodynamic forces. Within the bed, individuals are protected from drag and accelerational forces by their upstream neighbors (**Figure 2a**). However, pressure in the fast-moving water above the bed is lower than that in the sluggish water in the bed’s interstices, and this pressure gradient applies a lift force that tends to pull mussels away from the rock (Denny 1987). The larger the planform area of the mussel (approximately equal to the area of bed a mussel occupies), the greater the lift imposed. To cope with this size dependency, it is convenient to deal with lift in terms of hydrodynamic stress, i.e., the force per bed area. Hydrodynamic stress depends on the square of water velocity (Denny 1987, 1988; Vogel 1994), and water velocity is in turn proportional to the square root of wave height (Munk 1949, Denny 1988, Gaylord 1999). Thus, to a first approximation, hydrodynamic stress applied to mussels in a bed is directly proportional to wave height (Carrington 2002a, 2002b; Carrington et al. 2009).



**Figure 2**

(a) Mussels in the interior of a bed are subjected primarily to lift forces as water flows over the bed. (b) Each mussel is tethered to the substratum by its byssus. (c) *Inset*: A schematic depiction of the molecular structure of byssal thread proteins. Collagen polypeptides are flanked by a length of "precollagen" (represented in purple). In the distal portion of a thread, these precollagen blocks have sequences resembling spider silk. In the proximal portion of a thread, precollagen resembles elastin. Lengths of precollagen/collagen are likely crosslinked by disulfide bonds (S) and metal chelates and oxidized DOPA residues (M). Redrawn from Waite (1992). *Graph*: Distal and proximal portions of a byssal thread have different mechanical properties. The proximal portion is weaker and more compliant than the distal portion. However, the stiffer, stronger, and apparently oversized distal portion "yields" at a force less than that required to break the proximal portion. Note that the proximal portion is shorter than the distal portion; relative to its length, the proximal portion extends farther before breaking. Redrawn from Bell & Gosline (1996). (d) Observed extents of mussel dislodgment approximately match rates predicted by an ecomechanical approach for beds in Rhode Island. Adapted with permission from Carrington et al. 2009, copyright 2009 by the American Society of Limnology and Oceanography, Inc.

Local topography of the shore can modify this simple relationship. As with coral reefs, wave breaking can limit the height of waves that directly interact with intertidal sites (Helmuth & Denny 2003): Waves higher than this limit simply break farther offshore. Small-scale promontories and vertical walls can locally amplify velocity, resulting in an increase in stress (Denny et al. 2003), and stress is reduced in the lee of small-scale obstructions (O'Donnell 2008). These complexities require one to measure the relationship between wave climate and inshore velocity empirically for each site. Once this relationship is established, however, the hydrodynamic stress applied to a bed can be predicted for any wave conditions.

## Tenacity

The question, then, is whether the attachment of a mussel to the substratum is strong enough to resist this stress. The answer to this question requires detailed knowledge of the byssus, the “beard” of threads that tethers a mussel to the rock (**Figure 2b**). The strength of this tethering system varies among species, depending on the mechanical properties and size of each individual thread and the number of threads in the byssus (Bell & Gosline 1997, Brazee & Carrington 2006, Zardi et al. 2006). We explore each of these factors in turn before returning to the ultimate question of dislodgement and its implications for understanding distributional patterns and responses to climate change.

Each byssal thread comprises an adhesive plaque that attaches the thread to the rock or an adjacent mussel; a sleek, thin, distal portion; and a corrugated, thicker, proximal portion (**Figure 2b**). The base of each thread attaches to the byssal stem, which in turn attaches to the mussel’s body via the byssal root and retractor muscles. Each thread is formed separately by the mussel’s foot, where, in a process resembling polymer injection molding, chemical precursors of the thread mix and congeal in a specialized groove.

Owing in large part to the work of Waite and colleagues (e.g., Waite 1992, Waite et al. 1998, Lin et al. 2007), we know much about the chemical composition and macromolecular structure of byssal threads. Plaques adhere to the substratum with a protein glue that sticks to virtually any surface, and mussels vary the composition of plaque proteins to suit the substratum (Florioli et al. 2001). The long distal portion of the thread is formed primarily of a block copolymer (a molecular analogue of fiberglass) in which a silk-like protein (the analogue of glass fibers) controls stiffness and extensibility, and collagen (the analogue of the matrix surrounding the fibers) acts as a “filler” (**Figure 2c**, inset). The short proximal portion of the thread is formed of block copolymer with collagen again as the filler, but in this case, collagen is coupled with proteins that resemble elastin (the elastic protein of vertebrate circulatory systems) (Wainwright et al. 1976). The flow environment affects the chemical cross-linking by which precursor molecules form a viable thread (McDowell et al. 1999, Sun et al. 2001). Threads are also strongest when first produced and then degrade with time (Moeser & Carrington 2006). The rate of degradation varies seasonally, but the precise time course and basis of the degradation is uncertain.

The chemical differences between distal and proximal thread segments lead to distinct mechanical properties. The proximal portion has high extensibility, but relatively low stiffness and strength (**Figure 2c**). It is here—or in the adhesive plaque—that threads usually break. The distal portion is stronger than other components and, in this respect, is overdesigned. But the distal portion also has the important ability to “yield”: At a force that can still be resisted by the proximal segment, the distal thread abruptly increases its length (**Figure 2c**). This yield behavior ensures that the hydrodynamic load is shared evenly among threads in the byssus: If one thread is loaded disproportionately, it yields, allowing other threads to take up the slack. The combination of distal and proximal mechanical properties thus produces a byssus that is both stronger and less sensitive to the direction of applied force than would otherwise be the case (Bell & Gosline 1996).

We now pick up our discussion of the strength of the byssus as a whole, and begin by defining an important term—tenacity. In general, larger mussels have stronger tethers, and (as with the definition of hydrodynamic stress) it is again convenient to cope with this size dependency by expressing attachment strength as a function of the area of bed occupied by an individual. We thus define the tenacity of a mussel as the force per bed area required to dislodge it. If the hydrodynamic stress imposed on a mussel exceeds its tenacity, the animal is dislodged.

For a given species and environment, thread cross-sectional area increases approximately linearly with planform area as mussels grow (Carrington 2002b). Thus, tenacity is roughly constant



with increasing size even though the number of threads in the byssus does not increase. However, both the number of threads and the cross-sectional area of each thread commonly vary in apparent response to flow. For example, solitary mussels (which experience relatively large hydrodynamic forces) have more byssal threads than do bed mussels (Bell & Gosline 1997; Zardi et al. 2006, 2007), and the thickness of threads can increase with wave exposure (Zardi et al. 2006). The precise effect of flow on behaviors tied to thread production is still being determined (Moeser et al. 2006, Carrington et al. 2008).

Within a species, tenacity typically varies with season (Price 1980, Hunt & Scheibling 2001, Carrington 2002a, Lachance et al. 2008, Carrington et al. 2009). This variation may be due, in part, to behavioral responses (e.g., increased thread synthesis) to seasonal variation in wave exposure, but other factors are likely involved. For example, the production of byssal threads is metabolically costly—8% to 15% of a mussel's overall energy expenditure (Griffiths & King 1979)—and if food intake is limited, the energy of thread production must be traded against energy used for growth or reproduction. Mussels may respond to this trade-off by producing threads of inferior mechanical quality (Moeser & Carrington 2006).

## Predicting Dislodgment

Our developing mechanistic understanding of hydrodynamic stress and byssal tenacity allows us to predict the timing and magnitude of mussel dislodgment (e.g., **Figure 2d**), and these predictions provide ecological insight. For example, it has commonly been assumed that the rate of dislodgment is maximal during winter storms (e.g., Denny 1995). Indeed, in Rhode Island, winter storms impose large hydrodynamic forces. However, because tenacity is highest in winter in Rhode Island, these storms cause little dislodgment. Hurricanes produce waves of severity similar to that of winter storms, but they occur in late summer and early fall. In Rhode Island, because tenacity is minimal during that period, hurricanes can cause catastrophic dislodgment (Carrington 2002a, 2002b; Carrington et al. 2009). In short, it is the co-occurrence of large waves and low tenacity (rather than either factor alone) that has ecological consequence.

Our understanding of mussel mechanics also provides insight into processes of species invasion. The mussel *Mytilus galloprovincialis* is a potent invader, having dispersed from its Mediterranean origin to shores as widely spread as Great Britain, South Africa, and the west coast of North America. Its invasive abilities are mechanically limited, however. For a given shell length, *M. galloprovincialis* occupies more substratum area and has a weaker byssus than the native South African mussel *Perna perna* (Zardi et al. 2006, 2007). The reduction in byssal strength in *M. galloprovincialis* may be due to its increased relative rate of reproduction: When food intake is limited, *M. galloprovincialis* directs more energy to gonad production than does *P. perna*, apparently curtailing the production of byssal threads.

These mechanical and physiological factors provide predictions as to where *M. galloprovincialis* can and cannot invade. On the southern shores of South Africa, low food availability and the resulting low tenacity prohibit *M. galloprovincialis* from invading areas of high wave exposure (Zardi et al. 2007). On the western shores of South Africa, an area of high food availability, *M. galloprovincialis*' tenacity is comparable to that of *P. perna* and it can invade owing to its greater fecundity. On the west coast of North America, *M. galloprovincialis* is gradually replacing its congener *M. trossulus*, but even when well fed, *M. galloprovincialis*' adhesive tenacity is substantially less than that of the native *M. californianus* (Bell & Gosline 1997), preventing invasion on exposed shores.

If wave heights increase as a result of climate change (IPCC 2007), the worldwide invasion of *M. galloprovincialis* may recede from sites susceptible to increased water velocities. As the measurements of Helmuth & Denny (2003) show, however, this effect is likely to depend on local

**Turbulence:**

characteristic feature of fluid motion where chaotic, fine-scale eddies and vortices cause complex stirring and mixing

topography: If waves already break offshore at a site, any increase in wave height can have no additional effect.

There are gaps in our current understanding of mussel mechanics. In particular, the behavior of mussels within a bed is just beginning to be explored (e.g., Schneider et al. 2005), as are the consequences of mussel-to-mussel attachments (as opposed to mussel-to-rock attachments) and the mechanics of multilayer beds that lead to the formation of “hummocks,” areas of loosely attached mussels that protrude above the bed and provide initiation sites for catastrophic peeling of large patches. Lastly, and perhaps most importantly, the full gamut of physiological responses to the interactions among food availability, temperature, reproduction, hydrodynamic stress, and byssal strength remains to be determined.

## SPORE DISPERSAL AMONG KELP FORESTS

Kelp forests are one of the most important subtidal habitats along temperate shores (Foster & Schiel 1985), but their abundance varies dramatically through time. Storm waves, episodic nutrient limitation, and intense grazing can drastically decrease the density of local kelp populations (Dayton & Tegner 1984, Harrold & Reed 1985, Seymour et al. 1989, Dayton et al. 1992, Graham 1997), which may subsequently recover as spores from nearby forests wash in, settle, and grow. Because spore dispersal serves such an important role in the regional persistence of kelp forests (Reed et al. 2006), it has been a major focus in attempts to develop a quantitative understanding of kelp population structure and dynamics. However, because kelp spores are tiny (5–7  $\mu\text{m}$  in diameter), tracking or tagging is impractical, making estimation of dispersal distances difficult. This problem is now being confronted using mechanistic models of spore dispersal, allowing ecologists to address long-standing questions regarding kelp demographics and population connectivity.

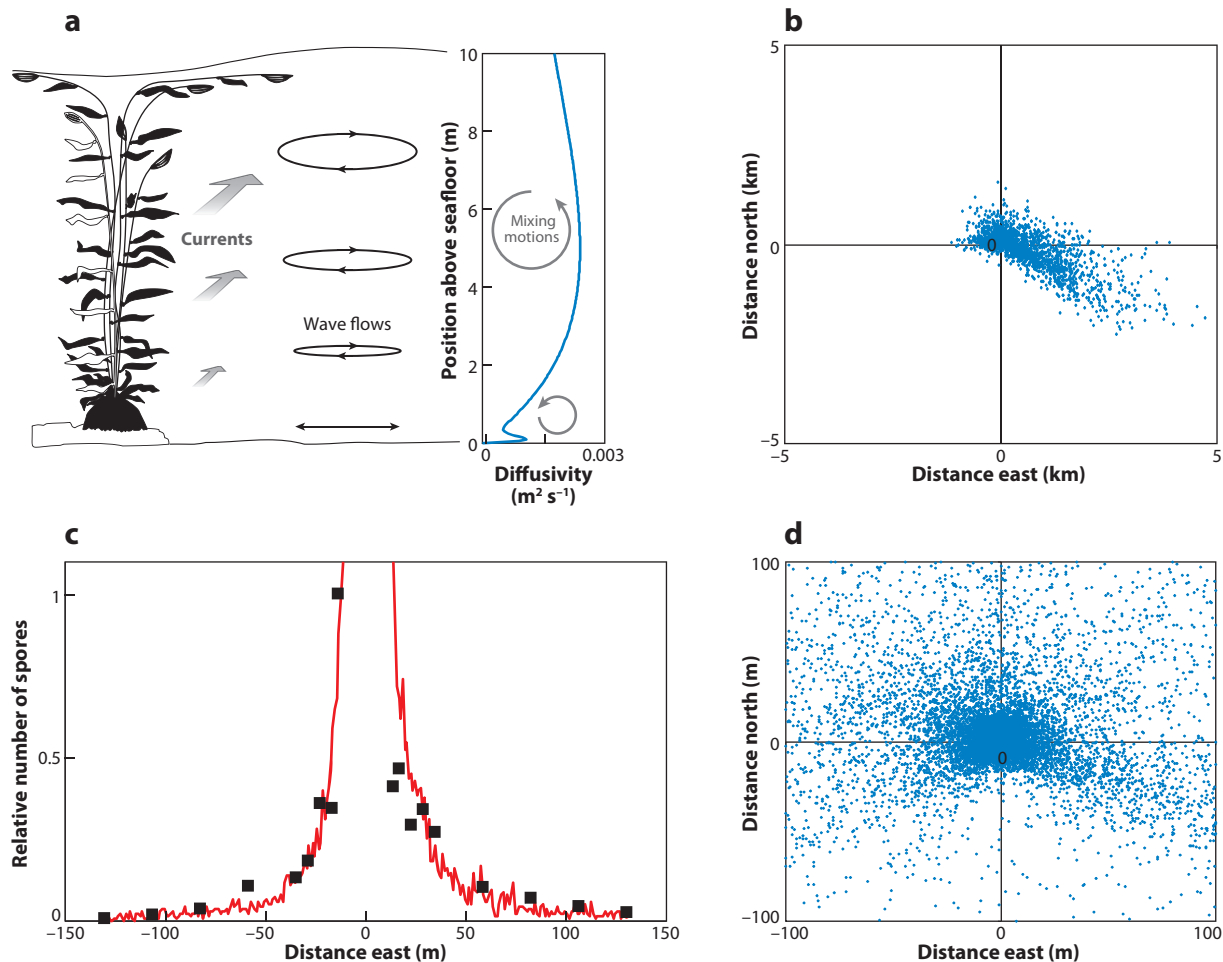
### Hydrodynamics

Transport of spores is driven primarily by coastal currents, which are themselves influenced by waves. Both currents and wave-driven flows are slowed by friction at the seafloor, which leads to a region of reduced velocity (a boundary layer) near the bottom (**Figure 3a**) (Schlichting 1979, Denny 1988). Boundary layers associated with currents may be several meters thick, creating the potential for very different dispersal scenarios for spores transported at various elevations in the water column. A second, much thinner (order 10 cm) boundary layer is generated by wave-induced flows, causing the current to behave as if the seabed were rougher than it actually is (Grant & Madsen 1986; Gaylord et al. 2002, 2006). The increased friction also enhances turbulence production at the seafloor, boosting hydrodynamic mixing and vertical movement of spores through the water column.

Rates of mixing are especially relevant for kelp spore dispersal because spores swim exceptionally weakly and are almost neutrally buoyant (Gaylord et al. 2002). Thus, spores reach the seafloor predominantly via stochastic turbulent fluid motions. In this respect, spore dispersal can be conceptualized in terms of a relatively simple cartoon: Vertical mixing dictates how long a spore remains aloft before it is brought to the seafloor, whereas horizontal currents determine how far a spore is carried during the intervening time between release and settlement.

### Kelp Reproduction

Physical transport and mixing processes also interact with kelps' life histories. Kelps have a two-phase life cycle that includes a macroscopic sporophyte stage (the conspicuous, canopy-forming



**Figure 3**

Physical factors dictating transport of spores and resultant patterns of dispersal. (a) Schematic showing how current speeds and orbital wave velocities vary with water depth and ensuing patterns of vertical mixing. Length scales of mixing are greater in the midwater column than near the seafloor, but intensities of mixing are higher near the seafloor. These factors produce a nonmonotonic mixing profile (eddy diffusivity profile). Eddy diffusivity values were calculated as in Gaylord et al. (2006) for conditions of  $2 \text{ cm s}^{-1}$  currents and 2-m waves with 10-s period, both interacting with a sandy seafloor (0.008 m roughness elements) as commonly occurs between forests. (b) A typical modeled spore dispersal distribution viewed as if from a satellite, demonstrating that transport can extend to several kilometers. (c) Observed (squares) and predicted (line) spore counts along the  $x$ -axis of panel b, demonstrating a rapid decline in settlement densities close to the source. (d) A “zoomed-in” depiction of settlement patterns in panel b, spanning a similar spatial extent as panel c. Data in panels b–d are redrawn after Gaylord et al. (2006).

stage), and a microscopic gametophyte. Male and female spores released by a sporophyte disperse, settle, and develop into microscopic male and female gametophytes, which subsequently produce gametes. Eggs extruded by female gametophytes are fertilized by sperm released from male gametophytes, but for this process to succeed, gametophytes must be close together: Spatial densities must exceed a critical threshold of  $1 \text{ mm}^{-2}$  (Reed 1990). Because of this density-dependent step, the maximal distance away from a source at which recruitment can occur depends on the number of spores released (Reed et al. 1997). If only a few spores are released, settlement rates

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**Random walk:**  
theoretical  
representation of  
turbulence where  
particles are  
transported in a series  
of randomly oriented  
steps

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even close to the parent may be insufficient to produce gametophyte densities high enough for fertilization. By contrast, if larger numbers of spores are released, two consequences may accrue. First, in the vicinity of parent kelps, high densities of gametophytes may lead to elevated rates of self-fertilization, with ensuing costs of inbreeding (Raimondi et al. 2004). Second, release of larger numbers of spores can lead to successful fertilization and eventual recruitment even at unexpectedly large distances from the parent kelps.

## Predictions

Trajectories of spore transport from release to settlement can be estimated using random-walk models (e.g., McNair et al. 1997) that capture the combined effects of horizontal currents, waves, and turbulent mixing. Such models indicate that spore dispersal distributions are extremely skewed (Gaylord et al. 2002, 2006). Many spores travel just a few meters, but a substantial fraction (the fat tail of the distribution) travel as far as kilometers (**Figure 3b–d**).

The random-walk models can also be merged with field data to estimate per-capita spore production, which is otherwise difficult to measure. Using the giant kelp, *Macrocystis pyrifera*, Gaylord et al. (2006) matched observed patterns of settlement to predicted distributions, and they scaled the rate of modeled spore release to appropriately align predictions with observations (**Figure 3c**). On the basis of this matching, they ascertained that giant kelps release approximately  $10^8$  spores per individual per day.

This tremendous rate of spore production acts in synergy with the shape of the dispersal distribution to foster connectivity among forests. Although early studies indicated that the majority of kelp recruitment occurs in close proximity to the adult source, often within a few meters (reviewed in Santelices 1990, Norton 1992), interpretation of results was hindered by the absence of a mechanistic framework. Recognition of the fat tail of the dispersal distribution provides evidence that, given their huge rate of production, spores can settle in densities sufficient for effective fertilization even at relatively large distances. Indeed, it appears that sufficient connectivity exists in many cases to allow modest-sized forests to facilitate recovery on denuded neighboring reefs as far away as several kilometers. These projections are consistent with widespread and nearly uniform kelp recruitment observed on virgin substrate several kilometers from source forests (Reed et al. 2004), a pattern less easily attributed to spore release from drifting kelp mats composed of a few reproductive individuals (Macaya et al. 2005, Hernandez-Carmona et al. 2006).

Related analyses also provide insight into rates of self-fertilization within forests. Given known dispersal distributions and rates of per capita spore production, settlement patterns from multiple source individuals can be overlain and the probability that fertilization occurs between gametes deriving from the same adult can be estimated. Such selfing rates depend on the spacing of adults within a forest, raising the possibility that even sparse kelp forests exhibit high rates of inbreeding. Preliminary calculations, for example, suggest that under certain conditions, levels of inbreeding can be quite high, of order 10% or more (Gaylord et al. 2006). Because inbreeding has striking costs to fitness in giant kelp—decreasing both survivorship and fecundity of selfed individuals—such relationships have the potential to introduce density-dependent feedbacks. Depending on population growth rates and the nature of such feedbacks, these relationships could conceivably induce population oscillations, regardless of the intensity of disturbance from extrinsic factors (Raimondi et al. 2004).

Climate-driven shifts in wave height and upwelling are likely to alter the intensity and consequences of physical disturbance in kelp forest systems. Prediction of these effects will require refined dispersal models that incorporate a range of physical and biological details. For example, large-scale circulation features and coastal geometries, both of which could alter connectivity

patterns, have not been included in existing analyses, and questions regarding secondary flows induced by the kelp's presence (Jackson & Winant 1983, Gaylord et al. 2007, Rosman et al. 2007) have yet to be addressed. These physical details have implications for the delivery of nutrients essential for growth and recruitment (Fram et al. 2008, Stewart et al. 2009), and for rates of self-fertilization through effects on within-forest transport (Graham 2003). The durations over which settled spores can survive as resting stages are incompletely understood but have consequences for density-dependent steps in recruitment and the buildup of genetically related spores around parent kelps (Ladah et al. 1999, Carney & Edward 2006), and these biological details warrant attention.

## EXTERNAL FERTILIZATION

Most benthic invertebrates reproduce by broadcast spawning, releasing their gametes into the water column and relying on fluid mixing to bring sperm and egg together. This process is thought to be inefficient if adults are spaced very far apart, leading to density-dependent Allee effects that have strong consequences for population demographics, particularly in harvested species that have artificially reduced densities (Quinn et al. 1993, Pfister & Bradbury 1996). The fraction of gametes that go unfertilized also has an important bearing on life-history evolution and the selection for certain reproductive strategies (Strathmann 1985, Havenhand 1995, Levitan 1995). However, beyond a simple awareness that external fertilization is variable and fraught with uncertainty, it has been difficult to develop from first principles both accurate estimates of the fraction of eggs that are fertilized and the relationship of this fraction to environmental factors. Marine ecomechanics is now making inroads to this fundamental problem, providing physically based understanding of processes operating at scales ranging from individual gametes to populations.

## Hydrodynamics

A primary characteristic of broadcast spawning is gamete dilution. The combination of molecular diffusion, turbulence, and shear dispersion ultimately produces a well-mixed, but more broadly dispersed, distribution of gametes. Prior to reaching the well-mixed stage, however, considerable structure may exist as gamete clumps are first stirred into distinct streaks and swirls that precede the development of a smooth concentration gradient (**Figure 4**) (Koehl et al. 2001, Crimaldi et al. 2002, Crimaldi & Browning 2004).

The process of stirring, spreading, and dilution tends to be rapid in the sea, but it can be counteracted if gametes are released within confined areas. Rocky coasts often have considerable topographic complexity, including embayments, surge channels, and tidepools of a variety of shapes and sizes. These features decrease rates of alongshore movement of water, thereby elevating durations over which substantial concentrations of gametes can be maintained at given locations as well as fertilization rates (Pennington 1985, Pearson & Brawley 1996, Serrao et al. 1996, Marshall et al. 2004). Rates of dilution can also be decreased if dispersion is reduced from a three-dimensional to two-dimensional process. The confinement of gametes to a single plane occurs in species (such as corals; e.g., Oliver & Willis 1987) that release buoyant gametes that float to the water's surface.

Although mixing and dilution proceed inexorably, some of their consequences for external fertilization can be offset over shorter timescales. The fine-scale structure of turbulent eddies is key in this regard. Because velocities associated with individual vortices or groups of vortices are correlated in space and time, they can foster localized, temporary convergence (coalescence) of sperm and egg clumps that were originally displaced relative to one another (**Figure 4d**). Thus, coherent structures in turbulence can counteract effects of dilution and dispersion over

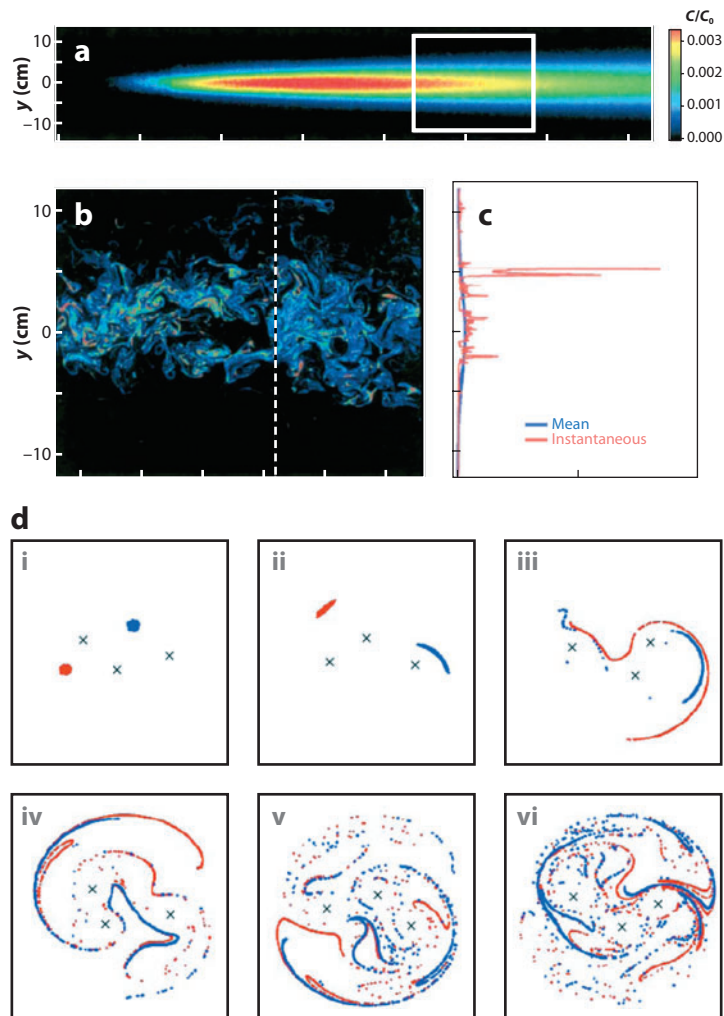
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**Allee effect:** tendency of some species to exhibit reduced population growth when at low densities

**Molecular diffusion:** process by which molecules spread over time as a result of random collisions

**Shear dispersion:** tendency for clouds of suspended material to be transported faster horizontally when higher in a bottom boundary layer, compared with material positioned closer to the bottom

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**Figure 4**

Mean and instantaneous structure in turbulent plumes. (a) Time-averaged solute concentrations (used as a physical analogy to gamete concentration) resulting from a constant rate of solute input into a laboratory flow. Concentration,  $C$ , is expressed relative to the undiluted concentration,  $C_0$ . (b) Instantaneous concentration field within the box shown in panel a. (c) Explicit comparison of the mean and instantaneous concentration profiles along the strip shown in panel b. (d) Numerical simulation showing how clumps of sperm and egg are stirred, forming streaks that can coalesce during early stages of mixing. The time sequence proceeds from panel i to panel vi, and the initial locations of the centers of three interacting vortices are depicted by  $x$  symbols. Panels adapted with permission from Crimaldi & Browning (2004).

small spatial and short temporal scales. This observation provides important insight because it directly countermands more traditional conceptualizations of turbulence based on simple diffusion analogies, which predict that concentrations of gametes vary smoothly in space and only decrease through time. Intriguingly, the common extrusion of gametes within viscous mucus (which one might naively think would inhibit fertilization) may also facilitate coalescence-enhanced fertilization by retarding rates of lateral movement of gametes out of turbulent structures (Thomas 1994, Crimaldi & Browning 2004). Mucus strands may furthermore decrease advective transport, and

thereby enhance local retention, via their tendency to become entangled on protruding bodies (e.g., spines of sea urchins) (Abelson & Denny 1998).

## Sperm-Egg Interactions

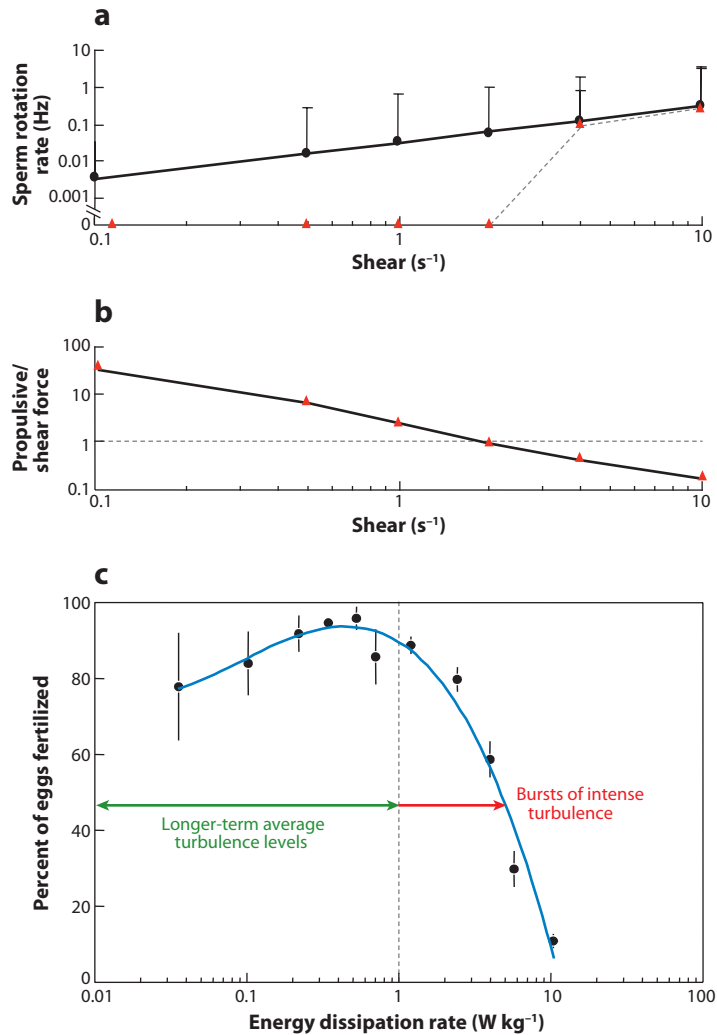
Sperm and eggs are smaller than all but the tiniest of turbulent structures in nature (Tennekes & Lumley 1972); therefore, biologists have traditionally assumed that gametes experience turbulence as a series of simple velocity gradients that change orientation and strength over time (Mann & Lazier 1996). Utilizing this convenient abstraction, Riffell & Zimmer (2007) demonstrated that, at relatively low shears common in subtidal habitats, sperm of the red abalone *Haliotis rufescens* can overpower fluid motion to maintain body position and follow chemical attractants emitted by an egg. At higher shears, in contrast, sperm swimming is too weak to maintain positioning and successfully navigate the steep velocity gradients formed around eggs. Although Jumars et al. (2009) recently noted that there is more flow structure at the scale of gametes than is often recognized, further evaluation will be required to determine the biological effects of this flow complexity.

## Estimating Fertilization Success

Ecomechanical prediction in the arena of external fertilization has not yet reached the same level as in other examples presented here. However, the potential for prediction exists, and considerable advances have emerged in some areas. For example, through the efforts of Riffell & Zimmer (2007), it is now possible to identify the hydrodynamic and locomotory criteria that dictate sperm-egg contact. Of particular importance is the ratio of sperm propulsive force to imposed fluid force, which determines whether a sperm can properly control its orientation within a shear field local to an egg (Figure 5a,b). The ecological relevance of these findings has also been determined. Mead & Denny (1995) and Denny et al. (2002) quantified fertilization outcomes when hydrodynamic forces overwhelm swimming capability. In cases of strong turbulence, where hydrodynamic shear around eggs is extreme, fertilization rates drop precipitously, from 90% to 10%. Analysis of surf-zone velocity records enables these laboratory results to be interpreted in a field context (Gaylord 2008). Particularly under larger waves, the intensity of surf-zone turbulence approaches levels that may have the capacity to impair fertilization (Figure 5c), even in the face of protective external layers on eggs that offset effects of shear (Thomas et al. 1999).

An important secondary issue in fertilization mechanics is that the time course of sperm-egg fusion may be critical. The highly intermittent character of turbulent velocity fluctuations produces brief bursts of intense shear that are layered onto longer-term, more benign values. If sperm-egg interactions are sensitive to transient bursts rather than average conditions, impacts of turbulence may be more pronounced than currently suspected. As our understanding of these relationships develops, it may become possible to address an important unknown in coastal marine ecology: For species that inhabit both intertidal and subtidal habitats, does reproductive success vary with level on the shore? In other words, do subtidal animals (living where turbulence is relatively weak) fertilize more readily than do intertidal animals? This issue could be of prime importance in determining how selection operates on relevant gamete traits, because selective pressures should vary strongly between these two environments.

In the examples discussed above, fertilization success is estimated through analysis of the small-scale details of turbulent flow. At larger scales, these details can, at times, be “averaged out” (e.g., Koehl et al. 1993, Koehl & Powell 1994), and for these greater distances and longer times, mixing models that emphasize time-averaged concentration fields provide predictive insight. Denny (1988) and Denny & Shibata (1989) computed patterns of gamete dispersion using classic



**Figure 5**

Effects of turbulent shear on sperm-egg interaction and fertilization rate. (a) Fluid shear can cause sperm to rotate in laboratory flows. Dead sperm (*black circles*) rotate in close accordance with theory (*solid line*), whereas live sperm (*red triangles*, *dashed line*) control their orientation and do not rotate except when shears are too strong. (b) The transition to conditions where sperm become unable to control their orientation occurs when shear forces exceed sperm propulsive forces. (c) Strong shears associated with intense turbulence (indexed by the rate at which kinetic energy is lost to viscosity, termed the energy dissipation rate) impair fertilization success in the laboratory, consistent with the inability of sperm to control orientation. Such turbulence levels also arise in nature, with longer-term average dissipation rates extending to  $1\ W\ kg^{-1}$  and short-term, intense bursts reaching  $10\ W\ kg^{-1}$ . Panels *a* and *b* redrawn with permission from Riffell & Zimmer (2007). Panel *c* redrawn from Mead & Denny (1995), Denny et al. (2002), and Gaylord (2008).

representations of turbulent plumes (e.g., Csanady 1973). These models enable quantitative prediction of the spatial scales over which gamete plumes extend, and they have been used advantageously in numerous field, laboratory, and numerical studies of effects of population abundance and spacing on fertilization success (e.g., Levitan 1991, Levitan et al. 1992, Babcock et al.



1994, Levitan & Young 1995, Coma & Lasker 1997, Metaxas et al. 2002, Yund & Meidel 2003, Lauzon-Guay & Scheibling 2007, Yund et al. 2007). The coupling of such models with empirical data may be especially useful as marine reserves are increasingly used as conservation devices, since they rely critically on proper assessment of threshold densities at which population-level reproduction becomes degraded.

There is also evidence that gametes can remain viable for much longer than is often appreciated (Bolton & Havenhand 1996, Meidel & Yund 2001, Johnson & Yund 2004). Under such conditions, if eggs are retained in shoreline embayments within the vicinity of spawning males, fertilization success can be appreciable. The mechanistic studies of Denny et al. (1992) provide initial predictions of the magnitudes of such effects in rocky shore habitats, complementing other studies in tidepools (e.g., Pennington 1985, Serrao et al. 1996, Marshall et al. 2004).

Complete vertical integration of fertilization mechanics from small-scale chemical sensing to the population scale is not yet possible. Considerable progress has been made toward understanding gamete coalescence at fine scales, but further work is required to extend existing insights (largely developed using two-dimensional numerical simulations) to conditions of more complex, three-dimensional turbulence. The temporal and spatial scales over which detailed turbulence structure is important also need to be quantified to determine when instantaneous versus time-averaged plume approaches offer the greatest utility.

## PREDICTING ECOLOGICAL EXTREMES

The physical environment plays an important (often controlling) role in ecological dynamics. As long as physiological thresholds are not exceeded (e.g., cooling to the point of freezing or heating to the point of death), the performance of individuals and the composition of communities are often well described by everyday conditions. However, nature is not without extremes: The environment can occasionally cause organisms to exceed their limits, resulting in ecological dynamics that depend more on the peaks of environmental factors than on their means (Gaines & Denny 1993). This leads to a fundamental problem: For any realistic distribution of events, extreme events are rare. So, how can we predict the extreme, but rare, events that strongly influence ecology?

Some extreme ecological events are “simple,” i.e., the result of a single environmental component. An earthquake, for example, can uplift a rocky bench, with profound and lasting ecological consequences on associated intertidal residents. Because they are rare and we lack a full mechanistic understanding of their causes, such simple events are difficult to predict. In contrast, many extreme ecological events result from the co-occurrence of well-understood, run-of-the-mill environmental factors. For instance, canyons in the American Southwest are subjected to infrequent brush fires and occasional rains, each of which by itself has little effect on stream insects. Stream water buffers lotic animals from the heat of a fire, and most of the water from even a torrential rain is absorbed by plants, thereby moderating storms’ effect on stream flow. Consequences are much more drastic, however, if by chance fire and rain occur in quick succession: Fire kills the plants, which are then unable to absorb the rain. The result is a flood that scours the streambed, extirpating stream insects and producing a long-lasting shift in stream community structure (Vieira et al. 2004). Paine et al. (1998) documented the many kinds of “ecological surprises” that can accrue from such compound extreme events.

### The Environmental Bootstrap

These sorts of compound events are open to prediction in ways that simple events are not. Denny et al. (2009) devised a statistical procedure (an “environmental bootstrap”) that allows estimation of

the probability that a compound extreme event will occur in a given period of time. The procedure begins with a short (5- to 10-year) time series of the relevant environmental factors and resamples the stochastic components of these factors to create a hypothetical year-long realization of how the environment could have played out differently. The procedure is repeated thousands of times, and a record is kept of the number of hypothetical years in which “normal” environmental factors co-occur to cause drastic ecological effects. The fraction of years containing such events is an estimate of the probability of their occurrence.

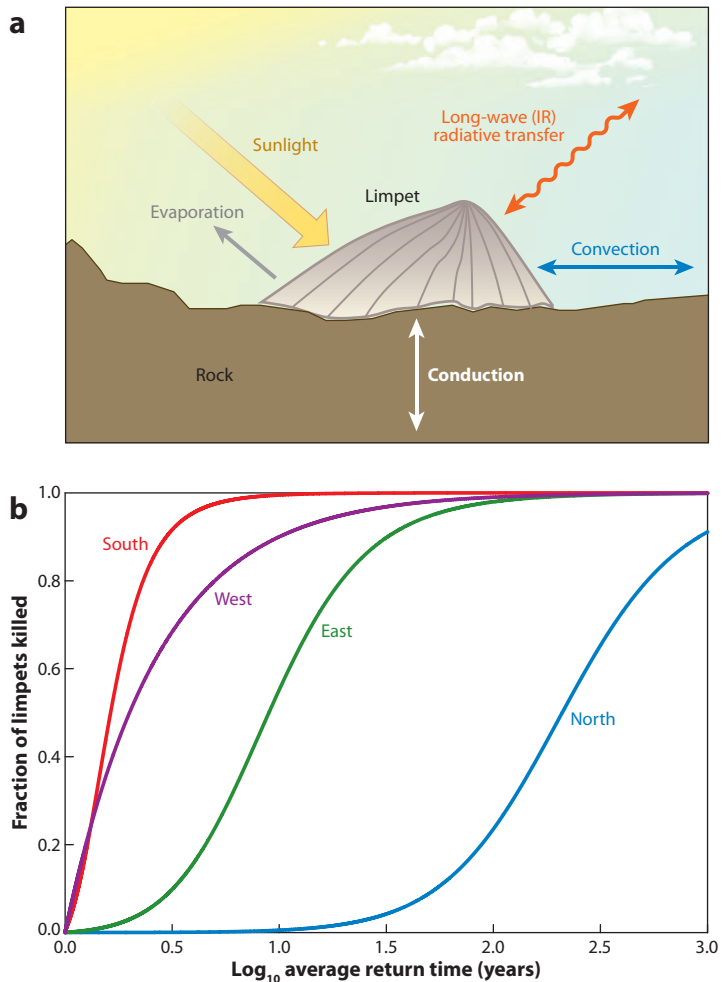
This procedure is straightforward if one knows the precise conditions that constitute an extreme ecological event. In many cases, however, this seemingly simple requirement is difficult to fulfill. For example, heat stress can kill intertidal limpets if a prolonged low tide coincides with bright midday sun, high air temperatures, low wind speeds, and a lack of wave splash (Denny et al. 2006). But there is a near-infinite combination of these parameters that may result in heat death: A slightly higher air temperature might compensate for a slightly lower solar irradiance, for instance. To successfully interpret such an environmental record, we need a mechanism to translate any combination of physical factors into a single, meaningful biological index. In this example, we need a mechanistic model of limpet thermal dynamics that takes as its inputs solar irradiance, air temperature, wind speed, and wave height and then produces as its output an accurate estimate of limpet body temperature.

### The Role of Mechanistic Models

It is here that ecomechanics comes into its element. Because of its mechanistic approach, ecomechanics excels in the construction of models that translate environmental inputs to biologically meaningful outputs (Helmuth et al. 2005, Carrington et al. 2009, Helmuth 2009). In the case of limpet body temperature, for instance, one constructs a heat-budget model by, in essence, tallying up all the ways in which thermal energy can enter or leave a limpet’s body (**Figure 6a**) (Gates 1980, Campbell & Norman 1998, Denny & Harley 2006). For any set of environmental conditions, there is a unique body temperature at which heat input to the limpet is equal to heat outflow, and for small organisms such as limpets, this equilibrium temperature is the realized body temperature. Thus, from any time series of the appropriate environmental factors, thermal mechanics allows one to calculate the time series of body temperatures. If temperature exceeds the limpet’s thermal limit, the animal dies. Coupled with a hypothetical environmental time series from a bootstrap resampling, this heat-budget approach allows one to quantify the probability of encountering a thermal event that would catastrophically affect limpet populations.

### Predictions

Using this approach, Denny et al. (2009) showed that for the owl limpet, *Lottia gigantea*, the likelihood of such events varies with position on the local rock topography (**Figure 6b**). Limpets living on south-facing surfaces are subjected to temperatures sufficient to kill 50% of the population, with an average return time of just 1.6 years, a potentially important factor in the near exclusion of *L. gigantea* from south-facing rocks (Miller et al. 2009). *L. gigantea* is a competitive codominant with mussels for primary space on Central California shores, and its exclusion from southern exposures can thus have dramatic effects on the local community composition. On a north-facing rock, however, similar mortality of *L. gigantea* is predicted to occur only once every 209 years on average, and the community composition there can be much different. It would be difficult for an ecologist to document directly the rarity of extreme events on north-facing rocks, thus the ecomechanical approach provides information that would otherwise not be accessible.



**Figure 6**

(a) A variety of mechanisms exist for the transfer of heat between an intertidal organism and its environment. For any given set of environmental conditions, there is a unique body temperature at which heat gain is equal to heat loss. For small organisms (such as the limpet shown here) realized body temperature is equal to this equilibrium temperature. (b) Predicted frequency of lethal thermal events varies with the orientation of the surface on which a limpet lives. Return time is the average interval between events; the more drastic the event, the longer the return time. Limpets on south-facing rocks (red line) experience extreme thermal conditions most often, those on north-facing rocks (blue line), least often. Redrawn from Denny et al. (2009).

The basic method outlined by Denny et al. (2009) can be applied to a wide variety of ecological questions (e.g., the co-occurrence of high waves and high tide leading to patch formation in mussel beds, or the occurrence in quick succession of fire and rain leading to the scouring of stream beds). In each case, the basic requirements are a representative time series of the pertinent environmental parameters and a mechanistic model that combines those parameters to give a single, biologically relevant output.

The principal challenge in the application of this approach is physiological rather than mechanical (Helmuth et al. 2005, Somero 2005, Gilman et al. 2006, Gracey et al. 2008, Helmuth

2009). For example, despite the implication noted in the discussion above, there is no single lethal limit for limpet body temperature; the temperature required to kill a limpet depends on (at least) maximum temperature, the duration of elevated temperature, and the humidity of the limpet's surroundings (Miller et al. 2009). It seems likely that lethal temperature also depends on a limpet's thermal history. If the limpet has been previously stressed, its response to a single extraordinary thermal event may differ. It is currently difficult, however, to predict even the direction of this effect: Previous stress may trigger acclimatization, increasing the limpet's tolerance for high temperatures. Alternatively, accumulated damage from repeated sublethal stresses may reduce the animal's tolerance. The challenge, then, is to construct a mechanistic model of limpet thermal response analogous to the heat-budget model for body temperature (Helmuth 2009). Ideally, such a model would take as input any time series of body temperature and give as output the probability of death or some other ecologically important biological parameter such as reproductive output or grazing rate.

### SUMMARY POINTS

1. Marine ecomechanics strives (*a*) to understand the mechanisms through which the physical environment affects the distribution and abundance of marine organisms and (*b*) to use this understanding to predict how changes in the environment will impact individuals, populations, and communities.
2. The approach and principles of marine ecomechanics are general and can be applied in any environment. Consequently, the following points apply to ecomechanics writ large: marine, terrestrial, or aerial.
3. Ecomechanics is intrinsically integrative. Its physically based approach is ideal for examining connections across scales from molecular to global.
4. Ecomechanics is innately interdisciplinary. Its pursuit invites new and deeper collaboration among ecologists, oceanographers, physiologists, and biomechanicists, among others.
5. The ecomechanical approach and its resultant models allow accurate prediction of responses to environmental conditions that do not currently exist and of the frequencies and consequences of extreme ecological events even when these events occur too rarely to be readily observed.

### DISCLOSURE STATEMENT

The authors are not aware of any potential biases that might be perceived as affecting the objectivity of this review.

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## LITERATURE CITED

- Abelson A, Denny MW. 1998. The roles of hydrodynamic forces in the settlement of marine propagules. *Annu. Rev. Ecol. Syst.* 28:317–39
- Babcock RC, Mundy CN, Whitehead D. 1994. Sperm diffusion models and in situ confirmation of long-distance fertilization in the free-spawning asteroid *Acanthaster planci*. *Biol. Bull.* 186:17–28
- Barnes DJ, Lough JM. 1996. Coral skeletons: storage and recovery of environmental information. *Global Clim. Change Biol.* 2:569–82
- Bell EC, Gosline JM. 1996. Mechanical design of mussel byssus: material yield enhances attachment strength. *J. Exp. Biol.* 199:1005–17
- Bell EC, Gosline JM. 1997. Strategies for life in flow: tenacity, morphometry, and probability of dislodgment of two *Mytilus* species. *Mar. Ecol. Progr. Ser.* 159:197–208
- Bellwood DR, Hughes TP, Folke C, Nystrom M. 2004. Confronting the coral reef crisis. *Nature* 429:827–33
- Bolton TF, Havenhand JN. 1996. Chemical mediation of sperm activity and longevity in the solitary ascidians *Ciona intestinalis* and *Ascidella aspersa*. *Biol. Bull.* 190:329–35
- Brazee SL, Carrington E. 2006. Interspecific comparison of the mechanical properties of mussel byssus. *Biol. Bull.* 211:263–74
- Campbell GS, Norman JM. 1998. *An Introduction to Environmental Biophysics*. New York: Springer-Verlag
- Carney LT, Edwards MS. 2006. Cryptic processes in the sea: a review of delayed development in the microscopic life stages of marine macroalgae. *Algae* 21:161–68
- Carrington E. 2002a. Seasonal variation in the attachment strength of blue mussels: causes and consequences. *Limnol. Oceanogr.* 47:1723–33
- Carrington E. 2002b. The ecomechanics of mussel attachment: from molecules to ecosystems. *Integr. Comput. Biol.* 42:846–52
- Carrington E, Moeser GM, Dimond J, Mello JJ, Boller ML. 2009. Seasonal disturbance to mussel beds: field test of a mechanistic model predicting wave dislodgment. *Limnol. Oceanogr.* 54:978–86
- Carrington E, Moeser GM, Thompson SB, Coutts LC, Craig CA. 2008. Mussel attachment on rocky shores: the effect of flow on byssus production. *Integr. Comput. Biol.* 48:801–7
- Coma R, Lasker HR. 1997. Effects of spatial distribution and reproductive biology on in situ fertilization rates of a broadcast-spawning invertebrate. *Biol. Bull.* 193:20–29
- Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–10
- Connell JH, Hughes TP, Wallace CC. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol. Monogr.* 67:461–88
- Crimaldi JP, Wiley MB, Koseff JR. 2002. The relationship between mean and instantaneous structure in turbulent passive scalar plumes. *J. Turbul.* 3:1–24
- Crimaldi JP, Browning HS. 2004. A proposed mechanism for turbulent enhancement of broadcast spawning efficiency. *J. Mar. Syst.* 49:3–18
- Csanady GT. 1973. *Turbulent Diffusion in the Environment*. Boston: D. Reidel
- Dayton PK. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41:351–89
- Dayton PK. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. *Proc. Colloq. Conserv. Probl. Antarct.*, Blacksburg, pp. 81–96. Lawrence, KS: Allen Press
- Dayton PK, Tegner MJ. 1984. Catastrophic storms, El Niño, and patch stability in a Southern California kelp community. *Science* 224:283–85
- Dayton PK, Tegner MJ, Parnell PE, Edwards PB. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* 62:421–45
- Denny MW. 1987. Lift as a mechanism of patch initiation in mussel beds. *J. Exp. Mar. Biol. Ecol.* 113:231–45
- Denny MW. 1988. *Biology and the Mechanics of the Wave-Swept Environment*. Princeton, NJ: Princeton Univ. Press
- Denny MW. 1995. Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. *Ecol. Monogr.* 65:371–418

- Denny MW, Shibata MF. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *Am. Nat.* 134:859–89
- Denny MW, Dairiki J, Destefano S. 1992. Biological consequences of topography on wave-swept rocky shores: I. Enhancement of external fertilization. *Biol. Bull.* 183:220–32
- Denny MW, Nelson EK, Mead KS. 2002. Revised estimates of the effects of turbulence on fertilization in the purple sea urchin, *Strongylocentrotus purpuratus*. *Biol. Bull.* 203:275–77
- Denny MW, Miller LP, Stokes MD, Hunt LJH, Helmuth BST. 2003. Extreme water velocities: topographical amplification of wave-induced flow in the surf zone of rocky shores. *Limnol. Oceanogr.* 48:1–8
- Denny MW, Harley CDG. 2006. Hot limpets: predicting body temperature in a conductance-mediated system. *J. Exp. Biol.* 209:2409–19
- Denny MW, Miller LP, Harley CDG. 2006. Thermal stress on intertidal limpets: long-term hindcasts and lethal limits. *J. Exp. Biol.* 209:2420–31
- Denny MW, Hunt LJH, Miller LP, Harley CDG. 2009. On the prediction of ecological extremes. *Ecol. Monogr.* 79:397–421
- Done TJ. 1983. Coral zonation: its nature and significance. In *Perspectives on Coral Reefs*, ed. DJ Barnes, pp. 101–47. Manuka, Aust.: Brian Clouston Publ.
- Floriolli RY, von Langen J, Waite JH. 2001. Marine surfaces and the expression of specific byssal adhesive protein variants in *Mytilus*. *Mar. Biotechnol.* 2:352–63
- Foster MS, Schiel DC. 1985. The ecology of giant kelp forests in California: a community profile. *US Fish. Wildl. Serv. Biol. Rep.* 85, Washington, DC
- Fram JP, Stewart HL, Brzezinski MA, Gaylord B, Reed DC, et al. 2008. Physical pathways and utilization of nitrate supply to the giant kelp, *Macrocystis pyrifera*. *Limnol. Oceanogr.* 53:1589–603
- Gaines SD, Denny MW. 1993. The largest, smallest, highest, lowest, longest and shortest: extremes in ecology. *Ecology* 74:1677–92
- Gates DM. 1980. *Biophysical Ecology*. Mineola, NY: Dover
- Gaylord B. 1999. Detailing agents of physical disturbance: wave-induced velocities and accelerations on a rocky shore. *J. Exp. Mar. Biol. Ecol.* 239:85–124
- Gaylord B. 2000. Biological implications of surf-zone flow complexity. *Limnol. Oceanogr.* 45:174–88
- Gaylord B. 2008. Hydrodynamic context for considering turbulence impacts on external fertilization. *Biol. Bull.* 214:315–18
- Gaylord B, Denny MW. 1997. Flow and flexibility I: effects of size, shape, and stiffness in determining wave forces on the stipitate kelps, *Pterygophora californica* and *Eisenia arborea*. *J. Exp. Biol.* 200:3141–64
- Gaylord B, Reed DC, Raimondi PT, Washburn L, McLean SR. 2002. A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. *Ecology* 83:1239–51
- Gaylord B, Reed DC, Raimondi PT, Washburn L. 2006. Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. *Ecol. Monogr.* 76:481–502
- Gaylord B, Rosman JH, Reed DC, Koseff JR, Fram J, et al. 2007. Spatial patterns of flow and their modification within and around a giant kelp forest. *Limnol. Oceanogr.* 52:1838–52
- Gilman SE, Wethey DS, Helmuth B. 2006. Variation in sensitivity of organismal body temperature to climate change over local and geographic scales. *Proc. Natl. Acad. Sci. USA* 103:9560–65
- Gracey AY, Chaney ML, Boomhower JP, Tyburczy WR, Connor K, Somero GN. 2008. Rhythms in gene expression in a fluctuating intertidal environment. *Curr. Biol.* 18:1–7
- Graham MH. 1997. Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, USA. *J. Exp. Mar. Biol. Ecol.* 218:127–49
- Graham MH. 2003. Coupling propagule output to supply at the edge and interior of a giant kelp forest. *Ecology* 84:1250–64
- Grant WD, Madsen OS. 1986. The continental-shelf bottom boundary layer. *Annu. Rev. Fluid Mech.* 18:265–305
- Griffiths CL, King JA. 1979. Energy expended on growth and gonad output in the ribbed mussel *Aulocomyza ater*. *Mar. Biol.* 53:217–22
- Hanski I. 1999. *Metapopulation Ecology*. Oxford: Oxford Univ. Press
- Harrold C, Reed DC. 1985. Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* 66:1160–69

- Havenhand JN. 1995. Evolutionary ecology of larval types. See McEdward 1995, pp. 79–127
- Helmuth B. 2009. From cells to coastlines: How can we use physiology to forecast the impacts of climate change? *J. Exp. Biol.* 212:753–60
- Helmuth B, Kingsolver JG, Carrington E. 2005. Biophysics, physiological ecology, and climate change: Does mechanism matter? *Annu. Rev. Physiol.* 67:177–201
- Helmuth BST, Denny MW. 2003. Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces? *Limnol. Oceanogr.* 48:1338–45
- Hernandez-Carmona G, Hughes B, Graham MH. 2006. Reproduction longevity of drifting kelp *Macrocystis pyrifera* (Phaeophyceae) in Monterey Bay, USA. *J. Phycol.* 42:1199–207
- Highsmith RC. 1982. Reproduction by fragmentation in corals. *Mar. Ecol. Progr. Ser.* 7:207–26
- Hunt HL, Scheibling RE. 2001. Predicting wave dislodgment of mussels: variation in attachment strength with body size, habitat, and season. *Mar. Ecol. Progr. Ser.* 213:157–64
- IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate Change 2007: The Physical Science—Summary for Policy Makers*. Cambridge, UK: Cambridge Univ. Press
- Jackson GA, Winant CD. 1983. Effect of a kelp forest on coastal currents. *Cont. Shelf Res.* 2:75–80
- Johnson SL, Yund PO. 2004. Remarkable longevity of dilute sperm in a free-spawning colonial ascidian. *Biol. Bull.* 206:144–51
- Jumars PA, Trowbridge JH, Boss E, Karp-Boss L. 2009. Turbulence-plankton interactions: a new cartoon. *Mar. Ecol.* 30:133–50
- Kleypas JA, Buddemeir RW, Archer D, Gattuso J-P, Langdon C, Opdyke DN. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284:118–20
- Knowlton N, Jackson JBC. 2001. The ecology of coral reefs. In *Marine Community Ecology*, ed. MF Bertness, SD Gaines, ME Hay, pp. 395–422. Sunderland, MA: Sinauer
- Koehl MAR, Koseff JR, Crimaldi JP, McCay MG, Cooper T, et al. 2001. Lobster sniffing: antennule design and hydrodynamic filtering of information in an odor plume. *Science* 294:1948–51
- Koehl MAR, Powell TM, Dairiki G. 1993. Measuring the fate of patches in the water: larval dispersal. In *Patch Dynamics in Terrestrial, Marine, and Freshwater Ecosystems*. ed. J Steele, TM Powell, SA Levin, pp. 50–60. Berlin: Springer-Verlag
- Koehl MAR, Powell TM. 1994. Turbulent transport of larvae near wave-swept shores: Does water motion overwhelm larval sinking? In *Reproduction and Development of Marine Invertebrates*. ed. H Wilson, G Shinn, S Stricker, pp. 261–74. Baltimore, MD: Johns Hopkins Univ. Press
- Lachance AA, Myrand B, Tremblay R, Koutinovsky V, Carrington E. 2008. Biotic and abiotic factors influencing attachment strength of blue mussels *Mytilus edulis* in suspended culture. *Aquat. Biol.* 2:119–29
- Ladah LB, Zertuche-Gonzalez JA, Hernandez-Carmona G. 1999. Giant kelp (*Macrocystis pyrifera*, Phaeophyceae) recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997–1998. *J. Phycol.* 35:1106–12
- Lauzon-Guay JS, Scheibling RE. 2007. Importance of spatial population characteristics on the fertilization rates of sea urchins. *Biol. Bull.* 212:195–205
- Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15:237–40
- Levitan DR. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol. Bull.* 181:261–68
- Levitan DR. 1995. The ecology of fertilization in free-spawning invertebrates. See McEdward 1995, pp. 123–56
- Levitan DR, Sewell MA, Chia FS. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology* 73:248–54
- Levitan DR, Young CM. 1995. Reproductive success in large populations: empirical measures and theoretical predictions of fertilization in the sea biscuit *Chlypeaster rosaceus*. *J. Exp. Mar. Biol. Ecol.* 190:221–41
- Lin Q, Gourdon D, Sun C, Holten-Andersen N, Anderson TH, et al. 2007. Adhesion mechanisms of the mussel foot proteins mfp-1 and mfp-3. *Proc. Natl. Acad. Sci. USA* 104:3782–86
- Macaya EC, Boltana S, Hinojosa IA, Macchiavello JE, Valdivia NA, et al. 2005. Presence of sporophylls in floating kelp rafts of *Macrocystis* spp. (Phaeophyceae) along the Chilean Pacific coast. *J. Phycol.* 42:913–22

- Madin JS. 2005. Mechanical limitations of reef corals during hydrodynamic disturbances. *Coral Reefs* 24:630–35
- Madin JS, Black KP, Connolly SR. 2006. Scaling water motion on coral reefs: from regional to organismal scales. *Coral Reefs* 25:635–44
- Madin JS, Connolly ST. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* 444:477–80
- Madin JS, O'Donnell MJ, Connolly SR. 2008. Climate mediated changes to postdisturbance coral assemblages. *Biol. Lett.* 4:490–93
- Mann KH, Lazier JRN. 1996. *Dynamics of Marine Ecosystems*. Cambridge, UK: Blackwell Sci.
- Marshall DJ, Semmens D, Cook C. 2004. Consequences of spawning at low tide: limited gamete dispersal for a rockpool anemone. *Mar. Ecol. Prog. Ser.* 266:135–42
- Massel SR. 1996. *Ocean Surface Waves. Advanced Series on Ocean Engineering*, Vol. 11. Singapore: World Sci.
- Massel SR, Done TJ. 1993. Effects of cyclone waves in massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. *Coral Reefs* 12:153–66
- McDowell LM, Burzio LA, Waite JH, Schaefer J. 1999. REDO detection of cross-links formed in mussel byssus under high flow stress. *J. Biol. Chem.* 274:2093–95
- McEdward L, ed. 1995. *Ecology of Marine Invertebrate Larvae*. Boca Raton, FL: CRC Mar. Sci. Ser.
- McNair JN, Newbold JD, Hart DD. 1997. Turbulent transport of suspended particles and dispersing benthic organisms: how long to hit bottom? *J. Theor. Biol.* 188:29–52
- Mead KS, Denny MW. 1995. The effects of hydrodynamic shear stress on fertilization and early development of the purple sea urchin *Strongylocentrotus purpuratus*. *Biol. Bull.* 188:46–56
- Meidel SK, Yund PO. 2001. Egg longevity and time-integrated fertilization in a temperate sea urchin (*Strongylocentrotus droebachiensis*). *Biol. Bull.* 201:84–94
- Metaxas A, Scheibling RE, Young CM. 2002. Estimating fertilization success in marine benthic invertebrates: a case study with the tropical sea star *Oreaster reticulatus*. *Mar. Ecol. Prog. Ser.* 226:87–101
- Miller LP, Harley CDG, Denny MW. 2009. The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. *Funct. Ecol.* 23:756–67
- Moerer GM, Carrington E. 2006. Seasonal variation in mussel byssal thread mechanics. *J. Exp. Biol.* 209:1996–2003
- Moerer GM, Leba H, Carrington E. 2006. Seasonal influence of wave action on thread production in *Mytilus edulis*. *J. Exp. Biol.* 209:881–90
- Munk W. 1949. The solitary wave theory and its application to surf problems. *Ann. NY Acad. Sci.* 51:376–424
- Norton TA. 1992. Dispersal by macroalgae. *Br. Phycol. J.* 27:293–301
- O'Donnell MJ. 2008. Reduction of wave forces within patches in mussel beds. *Mar. Ecol. Prog. Ser.* 362:157–67
- Oliver JK, Willis BL. 1987. Coral-spawn slicks in the Great Barrier Reef: preliminary observations. *Mar. Biol.* 94:521–29
- Paine RT, Levin SA. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51:145–78
- Paine RT, Tegner MJ, Johnson EA. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1:535–45
- Pearson GA, Brawley SH. 1996. Reproductive ecology of *Fucus distichus* (Phaeophyceae): an intertidal alga with successful external fertilization. *Mar. Ecol. Prog. Ser.* 143:211–23
- Pennington JT. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biol. Bull.* 169:417–30
- Pfister CA, Bradbury A. 1996. Harvesting red sea urchins: recent effects and future predictions. *Ecol. Appl.* 6:298–310
- Price HA. 1980. Seasonal variation in the strength of byssal attachment of the common mussel *Mytilus edulis* L. *J. Mar. Biol. Assoc.* 60:1035–37
- Quinn JF, Wing SR, Botsford LW. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *Am. Zool.* 33:537–50
- Raimondi PT, Reed CD, Gaylord B, Washburn L. 2004. Effects of self-fertilization in the giant kelp, *Macrocystis pyrifera*. *Ecology* 85:3267–76
- Reed DC. 1990. The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology* 71:776–87



- Reed DC, Anderson TW, Ebeling AW, Anghera M. 1997. The role of reproductive synchrony in the colonization potential of kelp. *Ecology* 78:2443–57
- Reed DC, Kinlan BP, Raimondi PT, Washburn L, Gaylord B, Drake PT. 2006. A metapopulation perspective on patch dynamics and connectivity of giant kelp. In *Marine Metapopulations*, ed. JP Kritzer, PF Sale, pp. 353–86. San Diego, CA: Academic
- Reed DC, Schroeter SC, Raimondi PT. 2004. Spore supply and habitat availability as sources of recruitment limitation in the giant kelp *Macrocystis pyrifera* (Phaeophyceae). *J. Phycol.* 40:275–84
- Riffell JA, Zimmer RK. 2007. Sex and flow: the consequences of fluid shear for sperm-egg interactions. *J. Exp. Biol.* 210:3644–60
- Robles C, Desharnais R. 2002. History and development of a paradigm of predation in rocky intertidal communities. *Ecology* 83:1521–36
- Rosman JH, Koseff JR, Monismith SG, Grover J. 2007. A field investigation into the effects of a kelp forest (*Macrocystis pyrifera*) on coastal hydrodynamics and transport. *J. Geophys. Res.* 112:C02016. doi:10.1029/2005JC003430
- Santelices B. 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr. Mar. Biol. Annu. Rev.* 28:177–276
- Schlichting H. 1979. *Boundary-Layer Theory*. New York: McGraw-Hill
- Schneider KR, Wethey DS, Helmuth BST, Hilbish TJ. 2005. Implications of movement behavior on mussel dislodgment: exogenous selection in a *Mytilus* spp. hybrid zone. *Mar. Biol.* 146:333–43
- Seed R, Suchanek TH. 1992. Population and community ecology of *Mytilus*. In *The Mussel Mytilus: Ecology, Physiology, Genetics, and Culture*, ed. G Gosling, pp. 87–169. New York: Elsevier
- Serrao EA, Pearson G, Kautsky L, Brawley SH. 1996. Successful external fertilization in turbulent environments. *Proc. Natl. Acad. Sci. USA* 93:5286–90
- Seymour RJ, Tegner MJ, Dayton PK, Parnell PE. 1989. Storm wave induced mortality of a giant kelp, *Macrocystis pyrifera*, in Southern California. *Estuar. Coast. Shelf Sci.* 28:277–92
- Smith LD, Hughes TP. 1999. An experimental assessment of survival, reattachment and fecundity of coral fragments. *J. Exp. Mar. Biol. Ecol.* 235:147–64
- Somero GN. 2005. Linking biogeography to physiology: evolutionary and acclimatory adjustments of thermal limits. *Front. Zool.* 2:1742–50
- Sousa WP. 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15:353–91
- Stewart HL, Fram JP, Reed DC, Williams SL, Brzezinski MA, et al. 2009. Differences in growth, morphology and tissue carbon and nitrogen of *Macrocystis pyrifera* within and at the outer edge of a giant kelp forest in California, USA. *Mar. Ecol. Prog. Ser.* 375:101–12
- Strathmann RR. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annu. Rev. Ecol. Syst.* 16:339–61
- Sun C, Vaccaro E, Waite JH. 2001. Oxidative stress and the mechanical properties of naturally occurring chimeric collagen-containing fibers. *Biophys. J.* 81:3590–95
- Tennekes H, Lumley JL. 1972. *A First Course in Turbulence*. Cambridge, MA: MIT Press
- Thomas FIM. 1994. Physical properties of gametes in three sea urchin species. *J. Exp. Biol.* 194:263–84
- Thomas FIM, Edwards KA, Bolton TF, Sewell MA, Zande JM. 1999. Mechanical resistance to shear stress: the role of echinoderm egg extracellular layers. *Biol. Bull.* 197:7–10
- Tunnicliffe V. 1981. Breakage and propagation of the stony coral, *Acropora cervicornis*. *Proc. Natl. Acad. Sci. USA* 78:2427–31
- Vieira NKM, Clements WH, Guevara LS, Jacobs BF. 2004. Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshw. Biol.* 49:1243–59
- Vogel S. 1994. *Life in Moving Fluids*. Princeton, NJ: Princeton Univ. Press. 2nd ed.
- Wainwright SA, Biggs WD, Currey JD, Gosline JM. 1976. *Mechanical Design in Organisms*. Princeton, NJ: Princeton Univ. Press
- Waite JH. 1992. The formation of mussel byssus: anatomy of a natural manufacturing process. In *Results and Problems in Cell Differentiation*, ed. ST Case, 19:27–54. Berlin: Springer-Verlag
- Waite JH, Qin X-X, Coyne KJ. 1998. The peculiar collagens of muscle byssus. *Matrix Biol.* 17:93–106
- Yund PO, Meidel SK. 2003. Sea urchin spawning in benthic boundary layers: Are eggs fertilized before advecting away from females? *Limnol. Oceanogr.* 48:795–801

- Yund PO, Murdock K, Johnson SL. 2007. Spatial distribution of ascidian sperm: two-dimensional patterns and short vs time-integrated assays. *Mar. Ecol. Prog. Ser.* 341:103–9
- Zardi GI, Nicastrò KR, McQuaid CD, Rius M, Porri F. 2006. Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: constraints of an evolutionary strategy. *Mar. Biol.* 150:79–88
- Zardi GI, McQuaid CD, Nicastrò KR. 2007. Balancing survival and reproduction: seasonality of wave action, attachment strength and reproductive output in indigenous *Perna perna* and invasive *Mytilus galloprovincialis* mussels. *Mar. Ecol. Progr. Ser.* 334:155–63



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## Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at <http://marine.annualreviews.org/errata.shtml>