© 2023. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2023) 226, jeb245442. doi:10.1242/jeb.245442

REVIEW

# Of corpses, ghosts and mirages: biomechanical consequences of morphology depend on the environment

**M. A. R. Koehl**

## ABSTRACT

Organisms are subject to the laws of physics, so comparative biomechanics is a powerful approach for identifying basic principles that apply across taxa of how morphology affects performance of mechanical functions such as locomotion, feeding or resisting damage. Journal of Experimental Biology has been a leading journal for decades in publishing studies revealing such basic biomechanical principles. However, field studies of the physical environment, ecological interactions and life-history strategies of organisms reveal which aspects of their biomechanical performance are important to their success in different types of natural habitats, and thus enable us to design ecologically relevant laboratory experiments to understand biomechanical function. Because the fitness consequences of differences in morphology are affected by the biological and physical environment, biomechanics can be used to identify how physical constraints on the performance of organisms with different body plans in variable environments can affect evolution. I illustrate these points with examples from the literature that show how the biomechanical consequences of morphology depend on the ecology of the organisms. Knowledge of the temporal patterns of interactions of organisms with their physical and biological environments is essential for understanding their functional morphology as it changes during ontogeny, and it reveals constraints on their evolution.

**KEY WORDS: Mechanical ecology, Comparative biomechanics, Ecomechanics, Evolutionary biomechanics, Morphology, Microhabitat**

## INTRODUCTION

Vogel and Wainwright (1969) wrote in a biology lab manual, 'Structure without function is a corpse, and function without structure is a ghost'. Here, I argue that this sentence should also say '...and an organism without its environment is a mirage'. While a ghost is a disembodied spirit, a mirage is something that seems to be real or true but is not really so (https://www.macmillandictionary.com/us/dictionary/american/mirage). My message is that ecology can determine how morphology affects performance. My hope is that this understanding can be woven into future studies of the evolution of organism structure and biomechanical function.

Comparative biomechanics is the study of non-human model organisms to elucidate general principles that apply across taxa of how biological structure determines physical performance. Journal of Experimental Biology (JEB) is a leading journal in publishing comparative biomechanics studies that reveal basic physical rules about how morphology at the cellular, tissue and whole-organism levels affects the performance of mechanical functions such as locomotion, feeding or resisting damage. These physical principles are explained for biologists in textbooks (e.g. Alexander, 1968, 2003a; Wainwright, et al., 1976; Niklas, 1992; Vogel, 1994; 2013; Vincent, 2012). Such quantitative biomechanical rules enable us to identify which aspects of morphology have important effects on defined aspects of organism performance and which have minor consequences, and they also predict how size changes can lead to novel biomechanical functions (reviewed in Koehl, 1996, 2000).

Organism morphology and mechanisms of motion evolved in the messy natural world where living things interact with complex terrain, turbulent ambient water flow or wind, and other organisms. Therefore, to understand the functional consequences of various aspects of the morphology and motion of an organism, we must measure the physical and biological environment as it is encountered by the organism throughout its ontogeny, and we must determine which biomechanical functions are important to its growth, survival and fitness in its natural habitat. In this paper, I present examples of how coupling field studies of ecological interactions, life-history strategies and physical habitats of organisms with laboratory analyses of their biomechanics can improve or change our understanding of the performance consequences of their morphologies. My goal is not to provide a comprehensive literature review of this topic, but rather to use selected examples to illustrate ways in which insights in comparative biomechanics can come from interfacing with ecology. Another objective is to include a historical perspective that highlights early studies in which these ideas and approaches were introduced.

### The interface between comparative biomechanics and ecology

Research at the interface between biomechanics and ecology has enhanced our understanding of the function of both ecosystems and organisms.

Some ecologists recognized the importance of processes at the organismal level in determining the dynamics of populations, communities and ecosystems, and in affecting the distribution and abundance of organisms (e.g. Schoener, 1986; May et al., 1989; McGill et al., 2006; Kiørboe et al., 2018). 'Biophysical ecology' (Gates, 1975), which analyzes heat and mass exchange between organisms and the environment, shows how organismal-level physiology and behavior can affect ecological processes (e.g. Gates, 1980; Porter et al., 1975; Campbell and Norman, 1998; Helmuth et al., 2010; Monteith and Unsworth, 2013). Likewise, 'ecomechanics' (Bauer et al., 2020) explores how organismal-level biomechanical mechanisms affect ecological processes (reviewed by Koehl, 1989, 1996, 1999; Jumars, 1993; Koehl and Wolcott, 2004; Herrel et al., 2006; Denny and Gaylord, 2010; Denny and Wethey, 2001; Baskett, 2012; Gaylord et al., 2012; Denny, 2016). JEB published a Special Issue on ecomechanics in 2012

Department of Integrative Biology, University of California, Berkeley, Berkeley, CA 94720-3140, USA.

*Author for correspondence (cnidaria@berkeley.edu)

M.A.R.K., 0000-0002-0633-1623

('Biophysics, bioenergetics and mechanistic approaches to ecology'; Denny, 2012; Knight, 2012), and Denny (2016) has written an ecomechanics textbook.

Here, I complement the rich literature in biophysical ecology and ecomechanics by focusing instead on 'mechanical ecology' (Bauer et al., 2020), studies that investigate how the ecology of organisms determines their biomechanical performance (Koehl, 1996, 1999, 2010, 2022).

## Mechanical ecology: environment can determine how morphology affects performance

Knowledge of the natural history of organisms (where they live and what they do in their natural environments; Greene, 1994) enables us to identify ecologically important biomechanical functions, while field measurement of the time-varying biological and physical interactions of organisms in natural habitats during their ontogeny informs our design of biologically relevant laboratory studies of their biomechanical performance.

### Ecologically important aspects of biomechanical performance

Laboratory studies and mathematical models have revealed the basic physics of how organisms do mechanical tasks such as supporting their bodies, locomoting and feeding, but knowledge of the habitats and ecological roles of organisms is necessary to understand the selective pressures affecting their mechanical design. Field studies enable us to identify which aspects of biomechanical performance are important to the success of organisms in nature, saving us from studying irrelevant aspects of biomechanical function. Here, I mention a few examples focused on locomotion.

Early analyses of the physics of swimming by body undulation or flapping paddles considered steady-state locomotion and explored aspects of kinematics and morphology that maximized speed or reduced the cost to travel a distance (Lighthill, 1971; Weihs 1994; Webb, 1975; Webb and Weihs, 1983). However, for many swimmers, escape from infrequent attacks by predators is more important to fitness than efficient cruising, and the body designs and kinematics of such animals enhance their ability to accelerate (Daniel and Meyhofer, 1989), or reduce vulnerability to gape-limited predators (Domenici, 2003). Webb (1984) analyzed body designs and thrust-production mechanisms of diverse fish and found that fish that feed on widely dispersed food have body and fin morphologies that enhance efficient cruising, whereas fish that live in structurally complex habitats and eat non-evasive prey have features that improve maneuverability, and fish that eat locally abundant evasive prey have designs that enhance acceleration.

The pendulum model for walking (Alexander and Jayes, 1983) and the spring–mass model for running (Alexander, 1984; Blickham and Full, 1993) explain the basic mechanisms by which diverse legged animals move across flat substrata. However, in nature, organisms locomote over rough substrata and can be knocked over, so biomechanical analyses of how their body designs provide passive or dynamic stability (Jindrich and Full, 2002; Sponberg and Full, 2008; Li et al., 2019) are critical to understanding how their morphology affects ecologically relevant performance. Furthermore, knowledge of the habitats through which organisms move can reveal novel modes of legged locomotion. For example, crabs that scuttle along the substratum underwater use a 'punt and glide' mechanism of locomotion with different kinematics from those they use when running in air (Martinez et al., 1998), and cockroaches that scramble through narrow crevices switch from running to 'body friction legged crawling' (Jayaram and Full, 2016).

Most analyses of animal gliding define good performance as minimizing the vertical distance lost per horizontal distance traveled, which occurs when the lift-to-drag ratio is maximized (Pennycuick, 1968; Norberg, 1990). The enlarged webbed feet and skin flaps of 'flying frogs' that glide through forest canopies were thought to enhance their lift-to-drag ratio (e.g. Rayner, 1981), but field measurements of living frogs and wind-tunnel experiments with physical models showed that these features worsened their gliding performance, but made them aerodynamically unstable and thus very maneuverable when they reoriented their large feet (Emerson and Koehl, 1990; McCay, 2001). Field studies showed that flying frogs maneuver through complex forest canopies to travel to breeding ponds at night. Measurements of wind in the forest canopy showed that air motion turbulent enough to tumble a gliding frog occurs during the day, but not at night when the frogs are gliding (McCay, 2003). The discovery that maneuverability, rather than glide performance, was the ecologically relevant aspect of aerodynamic performance for forest-dwelling flying frogs suggested that this might also be true for feathered dinosaurs such as *Microraptor gui*, whose fossils were found in deposits with forest trees (Zhou et al., 2003). Like flying frogs, *M. gui* had large aerodynamic surfaces rearward of the center of mass, and wind-tunnel experiments with dynamically scaled physical models showed them also to be unstable and maneuverable (Koehl et al., 2011; Evangelista et al., 2014).

The aerodynamics of animal flight has mainly been studied in the laboratory in still air or in wind tunnels with smooth air flow, but in nature, flying animals and the complex vegetation through which they navigate are buffeted by turbulent wind (Burnett et al., 2020). Therefore, ecologically important aspects of flight performance in nature represent trade-offs between aerodynamic stability and the ability to navigate around obstacles and execute righting maneuvers. Radio tags used to track bumblebees in the field while wind speeds and turbulence intensities were recorded showed that bumblebees forage in windy conditions. Wind-tunnel measurements of their flight in different levels of environmentally relevant turbulence showed that active responses of the bumblebees (increasing wingbeat frequency; increasing stroke amplitude and asymmetry) enable them to fly in turbulence (Crall et al., 2017). In contrast, orchid bees improve their roll stability in turbulent wind by extending their hindlegs ventrally, but this increases drag and the power required to fly, and decreases airspeed (Combes and Dudley, 2009). The ability of hovering hummingbirds to vary wingbeat frequency and body orientation when hit by vortices enables them to harvest nectar from flowers in the wind (Ortega-Jimenez et al., 2014)

Experimental analyses and mathematical models of the biomechanics of swimming, flying and pedestrian locomotion are generally done for organisms that are not carrying loads. However, locomoting organisms in nature often carry ecologically important things (e.g. food, nesting materials, eggs or young) that affect their locomotory performance by increasing their mass, altering their shape and moving their center of mass. Load carrying decreases the speed and increases the energetic cost of flying at high Reynolds number (*Re*) by birds (reviewed in Alexander, 2004), bats (MacAyeal et al., 2011) and insects (Coelho and Hoagland, 1995; Dillon and Dudley, 2004; Altshuler et al., 2005), of swimming at intermediate *Re* by zooplankton (Svetlichny et al., 2017), of swimming at low *Re* by microorganisms (Yasa et al., 2018; Weibel et al., 2005), and of walking and running (Alexander, 2002). Biomechanical analyses revealed which aspects of morphology and kinematics are responsible for the reduced speed and/or increased mechanical work of locomotion while carrying loads (walking: Browning et al., 2007; Tickle et al., 2013; Huang and Kuo, 2014; flying: Nudds and Bryant, 2002; Hambly et al., 2004).

If load carrying hampers locomotion, this can affect the fitness of organisms by hindering escape from predators, reducing foraging effectiveness and increasing energy requirements. For example, female copepods carrying external egg cases have higher respiration rates, swim more slowly and are more vulnerable to capture by fish predators than are females without eggs (e.g. Mahjoub et al., 2011; Svetlichny et al., 2017). Similarly, choanoflagellates carrying captured bacterial prey on their collars swim more slowly and catch fewer prey per work done to create the feeding current than do choanoflagellates not carrying prey (H. Nguyen, E. Ross, R. Cortez, L. Fauci and M.A.R.K., unpublished data).

Studies of organisms that routinely carry cargos in nature reveal morphological and kinematic features that enhance load-carrying locomotory performance. For example, honeybees that carry pollen and nectar use short-amplitude, high-frequency wing strokes that are less energy efficient than the low-frequency, high-amplitude kinematics of flies, but that enhance their ability to carry extra weight (Altshuler et al., 2005). Wing flexibility also improves load lifting by bees (Mountcastle and Combes, 2013). Female mosquitoes must take off from a host after ingesting a blood meal without being killed by the host. Unlike flies that take off by first jumping up and then flapping their wings, mosquitoes at the start of take-off flap their wings to generate aerodynamic forces while extending their long legs, thereby minimizing forces their feet impose on the host's skin and reducing the chance of being felt and swatted (Muijres et al., 2017). The ratio of flight muscle mass to body mass determines the mating success of a male dance fly, which must fly while carrying the female with whom he is copulating and the food gift he used to entice her (Marden, 1989). Another ecologically important behavior of many organisms is quickly adding or removing a load (e.g. picking up or dropping prey or young, autotomizing an appendage or tail). These rapid changes in load bearing can cause sudden perturbations to locomotion, so analysis of responses to such perturbations by diverse animals reveals body designs and kinematics that make organisms robust to abrupt changes in mass (Jagnandan and Higham, 2018).

### Convergence of biomechanical designs in diverse organisms meeting similar ecological challenges

We can learn basic principles about biomechanical designs by studying features shared by different types of organisms performing similar ecological tasks. The shapes of suspension-feeding benthic animals in flowing water (Wainwright and Koehl, 1976) and pollen-catching structures of plants in wind (Niklas, 1982, 1985) cause flow patterns that enhance the capture of particles. The flexibility that permits passive reconfiguration of benthic animals (e.g. Koehl, 1977c) and macrophytes (e.g. Koehl, 1984, 2022; Carrington, 1990) in water currents, and of terrestrial plants in wind (e.g. Vogel, 1984), is an important drag-reducing mechanism for organisms attached to surfaces exposed to ambient flow. The shapes of wings and mechanisms of generating lift are similar for gliding plant seeds and animals (e.g. Lentink et al., 2009; Bauer et al., 2020). Diverse organisms, from protozoans to animals in different phyla, use arrays of fine cylinders to catch particulate food or to capture molecules from the surrounding water or air. All these diverse arrays of hairs are subject to the same physical rules that determine how morphology and kinematics affect the flow around or through the arrays (Cheer and Koehl, 1987; Koehl, 1992, 1995), whether they operate in water (e.g. Mead and Koehl, 2000; Koehl et al., 2001; Koehl, 2004; Reidenbach et al., 2008; Waldrop et al., 2015) or in air (e.g. Loudon and Koehl, 2000; Waldrop and Koehl, 2016). In addition, physical rules that apply to all these different hair arrays govern which mechanisms they use to catch particles and molecules (Rubenstein and Koehl, 1977; Shimeta and Jumars, 1991).

### Organisms alter the physical environment

The physical environment encountered by organisms is often modified by other organisms, so field studies should assess both the abiotic and biotic environment. Stands of sessile organisms alter wind or water flow through a habitat, thereby changing the conditions experienced by flying, swimming or running organisms, by dispersing seeds or spores, and by other sessile organisms. Both field measurements and mathematical models describe how terrestrial plant canopies, from forests to wheat fields, and aggregations of intertidal marine organisms in air at low tide reduce wind speeds and affect light, heat and humidity (Campbell and Norman, 1998; Monteith and Unsworth, 2013; Helmuth et al., 2010; Denny, 2016). Kelp beds and seagrass meadows slow water currents and damp waves (Jackson and Winant, 1983; Koehl and Alberte, 1988; Gaylord et al., 2003; Koch et al., 2006; Koehl, 2022), as do coral reefs (Koehl and Hadfield, 2004; Reidenbach et al., 2006). Sessile organisms living alone or at the edges of aggregations have less protection from fluid dynamic forces or desiccation than do those in the middle, which instead suffer depletion of air- or water-borne resources by upstream organisms (bryozoans: Okamura, 1984; mussels: Okamura, 1986; seagrass: Fonseca et al., 2019). Solitary and edge-dwelling individuals can have different morphologies and biomechanical performance than do conspecifics in the middle of aggregations (e.g. Holbrook et al., 1991; Koehl and Silk, 2021). The environment encountered by epibionts living on a sessile organism depends both on the flexibility of the host and on whether the host is in an aggregation (Koehl and Daniel, 2022).

Infaunal organisms alter the physical environment of sedimentary habitats. Burrowing animals change the cohesion and compaction of marine mud (Clemo et al., 2022). Tube-building marine worms affect local flow velocities along sediment surfaces that alter patterns of deposition and resuspension of particles and microorganisms, thereby affecting food availability for benthic suspension feeders (Eckman, 1985; Johnson, 1990).

Groups of swimming or flying organisms affect water or air motion. Swarms of swimming zooplankton increase mixing of water in the ocean (Dabiri, 2010; Katija, 2012). Flow generated by animals swimming in schools alters the cost of swimming in ways that depend on their arrangement and spacing (Weihs, 1975; Liao, 2007; Pan and Dong, 2020; Catton et al., 2011; Saadat et al., 2021). Air flow in flocks of flying birds (Lissaman and Shollenberger, 1970; Usherwood et al., 2011) and swarms of flying insects (Ahmed and Faruque, 2022) depends on the arrangement of individuals relative to each other and can affect flight aerodynamics and stimulate changes in wing kinematics.

### Environment can modify organism morphology and mechanical properties

To understand the biomechanical performance of organisms in nature, we should determine whether their morphology or mechanical properties are altered by their environment. Interaction with the environment sometimes can improve biomechanical performance. Radular teeth of some gastropods have a microarchitecture that causes them to be sharpened as they are abraded during grazing (Padilla, 1985; Wang et al., 2014).

Barnacles at wave-exposed sites are chipped by small water-borne debris into shapes that are more resistant to crushing by logs slammed onto the shore by waves (Pentcheff, 1991). In contrast, when kelp fronds are knotted and tangled as they are whipped back and forth by waves, hydrodynamic forces on them increase (Burnett and Koehl, 2019). Epibionts raise hydrodynamic forces on their hosts by increasing host stiffness and/or size (Koehl and Daniel, 2022). Herbivore damage of macroalgae produces weak spots where they are likely to break when exposed to ambient water flow (Burnett and Koehl, 2022). Sometimes, pruning by herbivores reduces hydrodynamic forces on macroalgae and improves their chances of surviving big waves (Black, 1976), while in other cases, breakage at herbivore wounds is an important cause of mortality (Koehl and Wainwright, 1977; Burnett and Koehl, 2020). Ocean acidification weakens calcified skeletons and shells of some marine organisms, but not others (Kroeker et al., 2010), and reduces the strength of byssal threads attaching mussels to the shore (O'Donnell et al., 2013).

Some organisms remodel themselves in response to cues from the environment (West-Eberhard, 2003). Macroalgae provide examples of such plasticity. Some respond to herbivore damage by increasing the strength and toughness of their tissues (Lowell et al., 1991) or by widening their support structures (Burnett and Koehl, 2019). The magnitude of tensile stress in kelp blades due to hydrodynamic forces induces the blades to grow into shapes that enhance performance in their local water flow habitat (Koehl and Alberte, 1988; Koehl and Silk, 2021).

### Microhabitats

Diverse organisms living at the same site can experience very different physical conditions. Striking examples of microhabitats are provided by bottom-dwelling marine organisms. Water flowing along a surface is slowed, so a velocity gradient develops between the substratum and the freestream current; short organisms in this 'benthic boundary layer' encounter slower flow than their taller neighbors (e.g. Koehl, 1982; Jumars and Nowell, 1984). Local topography and nearby organisms also alter the ambient flow experienced by an organism. Thus, on a coral reef exposed to waves with peak freestream velocities >1 m s$^{-1}$, a sea urchin sitting on the top of the reef would encounter peak velocities of ~0.3 m s$^{-1}$ (Fig. 1A), while a microscopic larva would experience peak velocities of only 0.1 m s$^{-1}$ (Fig. 2A). However, within the reef between coral branches, an urchin would see peak velocities of only ~0.08 m s$^{-1}$ (Koehl and Hadfield, 2004), while a larva would experience peaks of ~0.02 m s$^{-1}$ (Fig. 2A). Furthermore, hydrodynamic forces hitting the shore vary on spatial scales of centimeters as a result of substratum topography and the complexity of turbulent waves (Gaylord, 2000; O'Donnell and Denny, 2008). An example of quantifying spatial variation on a shore of physical features (e.g. topography, wave force, temperature) and biological parameters (e.g. species diversity, recruitment, predator abundance) is given in Denny et al. (2004).

Organisms can inhabit similar microhabitats at sites exposed to different physical conditions. Motile animals seek microhabitats with suitable conditions and sessile organisms can change the microhabitat they experience by altering their morphology. For example, sea anemones experience maximum velocities of ~0.1 m s$^{-1}$, both when assuming short postures on the floor of surge channels exposed to waves with peak freestream velocities of ~6 m s$^{-1}$, and when standing taller at protected sites washed by small waves with peak freestream velocities of only ~0.5 m s$^{-1}$ (Koehl, 1977a).

### Temporal scales and biomaterial mechanics

Most biomaterials (tissues, skeletal materials, secretions) have strain- and time-dependent mechanical properties that vary with temperature (e.g. Wainwright et al., 1976; Vincent, 2012). Thus, their stiffness, resilience, strength, extensibility and toughness in natural habitats depend on temperature and on the rates, durations and frequencies of forces they experience. For example, the connective tissue (mesoglea) of the body wall of a hydrostatically supported sea anemone is viscoelastic. Materials-testing procedures

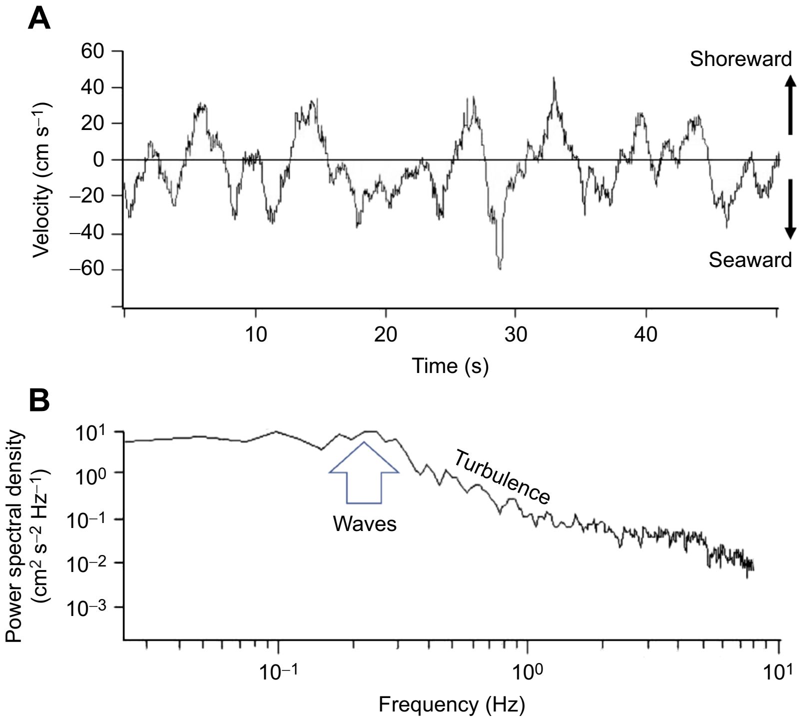

**Fig. 1. Water velocity measured using acoustic Doppler velocimetry 0.02 m above the top of a coral reef subjected to turbulent waves.** (A) Shoreward (positive values) and seaward (negative values) water velocity plotted as a function of time. (B) Spectrum of a 6 min record of velocity showing how much of the variation in velocity is due to fluctuation at different frequencies.

that simulated the magnitude, frequency and duration of different mechanical stresses on mesoglea in nature showed that it is stiff and resilient when subjected to brief stresses simulating muscle contraction or repetitive battering by waves, is compliant when subjected to steady stress in a tidal current lasting a few hours that reshapes anemones into configurations that enhance prey capture, and is extended to twice its resting length when subjected for 24 h to low stress due to the small internal pressures sea anemones use to inflate themselves (Koehl, 1977b). The strength of byssal threads that mussels use to attach themselves to the shore is greater at high strain rates, so they are most resistant to breaking when exposed to rapid loading when hit by waves (Carrington and Gosline, 2004). Frond tissue of some macroalgae is stronger when stretched rapidly to simulate wave impingement than when pulled more slowly (Burnett and Koehl, 2021).

Animal activities can affect mechanical properties of biomaterials. The cuticle between segments of a female locust's abdomen is a stress-softening material, so its stiffness decreases and extension increases if it is subjected to repeated cycles of being stretched to a stress higher than the peak of the previous cycle (Vincent, 1975). When inserting their abdomens into the ground to deposit eggs, locusts stretch and relax their abdomens in this cyclic way, so stress softening enables them to stretch their abdomens to much greater lengths than would be possible with one steady extension. Mollusk shell has a high breaking strength when exposed to a single application of force (Currey and Taylor, 1974), but when predatory crabs use their claws to break clam shells, they repeatedly squeeze the shells at stresses lower than breaking stress. Under this repetitive loading, the shell material accumulates small cracks that eventually cause fatigue fracture (Boulding, 1984). Other examples of how predation success is affected by the time dependence of biomaterial properties are reviewed in Higham et al. (2021).

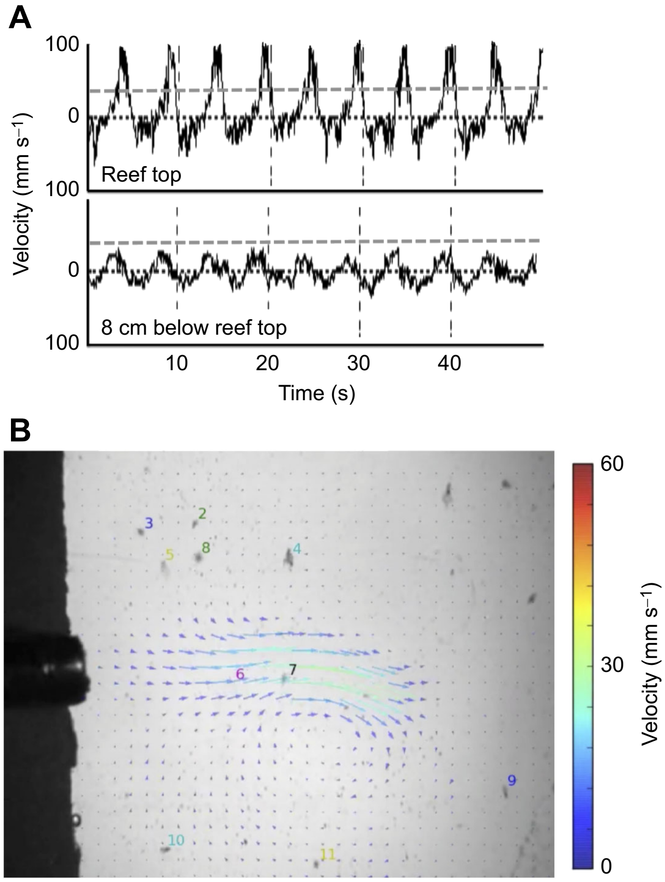

**Fig. 2. Water velocities encountered by microscopic larvae of *Phestilla sibogae* crawling on coral.** (A) Laser Doppler velocimetry (LDV) measurements of water velocity in a wave flume 200 µm from a coral surface (unpubished data from the study reported in Reidenbach et al., 2009) at the reef top, and 8 cm below the reef top. Water flows back and forth. Dotted line indicates zero velocity. Dashed line shows the peak velocity of a flow pulse that dislodges larvae of *P. sibogae* off a surface, measured using the device in B. (B) Frame of a video of *P. sibogae* larvae (numbered) crawling on a surface subjected to pulses of water flow like that shown in A. Colored arrows show instantaneous velocity vectors measured using particle image velocimetry (PIV) of 13 µm beads in the water.

### Life-history strategies and environmental stress factor

The likelihood that a structure will fail is given by its safety factor, the ratio of breaking stress (force per cross-sectional area) of its material to the maximum stress it experiences during its lifetime. Biological structures exposed to predictable stresses generally have lower safety factors than do those exposed to unpredictable stresses (Alexander, 1981). However, the size, shape and material properties of organisms change during ontogeny and differ between sites, and the mechanical stresses they experience change with the seasons. Therefore, an ecologically relevant measure of likelihood of failure is 'environmental stress factor' (ESF), the ratio of the breaking stress of a component of an organism at some stage in its life to the maximum stress experienced by that component as it functions in the habitat of the organism during that life stage (Johnson and Koehl, 1994). Morphologically plastic organisms such as kelp, which change their shape and material properties in response to environmental signals, can have the same ESF in different physical habitats (Johnson and Koehl, 1994). Because ESF can change during the life of an organism, low ESF correlates with the times during ontogeny and the seasons when organisms get broken (Johnson and Koehl, 1994; Stewart, 2006; Wolcott, 2007; Sirison and Burnett, 2020; Koehl and Daniel, 2022).

Organisms face trade-offs between investment in mechanical support versus investment in reproduction, and different life-history strategies balance these two factors. Some macroalgae grow quickly and reproduce before winter storms wash them away (low ESF in winter) (Johnson and Koehl, 1994; Koehl, 1999; Koehl and Daniel, 2022), while others grow slowly, producing strong thalli that survive storms (high ESF year round) and reproduce year after year (Koehl, 1999). Barnacle species in habitats with high levels of crab predation (low ESF year round) grow quickly, produce weak shells and reproduce early, whereas species not subjected to crab predation grow slowly, produce strong shells, live longer and reproduce later (Murdock and Currey, 1978). During winter, mussels increase their investment in byssal threads that anchor them to rocks, improving attachment strength twofold over their tenacity during summer and autumn, when they invest more in growth and reproduction. However, if big storms arrive early relative to this annual cycle in attachment strength, many mussels wash away (Carrington, 2002).

In some cases, 'bad' (from an engineering perspective) mechanical designs enhance ecological performance. Soft tunicate colonies attach to surfaces with weak glue, but this 'bad' glue protects them from damage when they are ripped off surfaces by ambient flow, enabling them to disperse to new habitats where they reattach to surfaces (Edlund and Koehl, 1998). For a coral with long, narrow branches that are easily broken by waves, this 'bad' design provides a mechanism of asexual reproduction and dispersal because the broken fragments survive and reattach to the reef (Tunnicliffe, 1981). 'Bad' engineering enhances reproduction and dispersal by an alga that increases its buoyancy and has weaker stipe tissue when it becomes reproductive. These reproductive algae are easily ripped off the substratum by ambient water flow and form floating aggregations where they shed gametes and are transported to new sites by currents (Stewart, 2006). Seagrasses use a similar strategy for long-distance dispersal (Harwell and Orth, 2002; Källströma et al., 2008), although some reproductive shoots are strong enough to persist at a site during storms (Patterson et al., 2001).

These examples illustrate the importance of considering how the timing of ontogenetic changes of organisms relates to the temporal patterns of environmental stresses they experience, and of understanding how the relationship between life-history strategy and mechanical design can affect the reproductive success and fitness of organisms.

## Meeting the challenges of mechanical ecology

Biomechanical studies in the field can be difficult, and studying biomechanical performance in the lab under ecologically relevant conditions can be tricky, but various approaches to these challenges have been developed.

### Measuring physical environments and organism mechanics in the field

Challenges to biomechanical research in the field range from carrying equipment across rough terrain or keeping electronics working underwater, to fending off attacks by territorial fish. When we pioneered field biomechanics, we used home-made force transducers (Koehl, 1977a; Denny, 1982) and flow meters (Koehl, 1976, 1977a; LaBarbera and Vogel, 1976), recording their output on audiotape. Today, technological advances in miniaturizing and weatherproofing electronics, transmitting and recording signals, and digital imaging enable us more easily to make a wide array of biomechanical measurements in the field (Denny, 2012; Bauer et al., 2020; Burnett and Gaylord, 2022), including particle image velocimetry (PIV) (Katija and Dabiri, 2008; Sutherland et al., 2011).

Biomechanics can also be done in natural habitats with inexpensive techniques useful for pilot studies and student field trips. Water flow is visualized using dye streams (Koehl, 1977d; Norton et al., 1982), and air flow by smoke streams (Kawai, 1981). The translation and expansion of dye blobs is used to quantify advection and turbulent diffusion of water-borne materials through a habitat (e.g. Koehl et al., 1993, 1997). Water or air velocity is measured by timing particles carried by the fluid across measured distances, or by deflection of calibrated flexible cantilevers bent by the flow (Koehl, 1977d). Weight-loss rates of Life Savers candy attached to organisms can be used to measure boundary shear velocities along their surfaces (Koehl and Daniel, 2022). Mechanical spring scales are used to measure peak water velocities (Bell and Denny, 1994), peak hydrodynamic forces on organisms (Koehl, 1999), and flexural stiffness (Koehl, 1977d) and attachment strength of organisms (Bell and Gosline, 1997; Koehl and Daniel, 2022).

### Identifying spatial and temporal scales relevant to organism function in natural habitats

Field studies reveal that the physical and biological environment of an organism vary on a wide range of spatial and temporal scales, while an organism's size, structure, behavior and ecological role can change during ontogeny. Therefore, when measuring environmental conditions, we must determine how the organism encounters its habitat. What is the spatial scale of the biomechanical process? What are the rates, frequencies and magnitudes of loads on the organism in nature? How does the environment vary from second to second, during a day, with the seasons, and year to year? How do these habitat variations relate to the timing of ontogenetic changes during the lifetime of the organisms?

Patterns of spatial and temporal variation of natural habitats can be described quantitatively using various approaches detailed by Denny (2016). Spectral analysis has long been used to identify the scales of variation in space or time of measured parameters in the environment (Platt and Denman, 1975). For example, the magnitude of ambient water velocity at a field site can be plotted as a function of time (Fig. 1A). A Fourier transform of such data decomposes the record into a series of waveforms of different frequencies and reveals how much of the total variance in velocity is due to fluctuations at each frequency (Fig. 1B). Statistical techniques can predict the occurrence of rare extreme environmental events that cause high mortality (e.g. violent wind gusts, huge ocean waves), which can be more important ecologically than average conditions (e.g. Denny et al., 2009; Denny and Dowd, 2012).

### Replicating field conditions on ecologically relevant scales in the laboratory

To illustrate in more detail some of the ways we can measure the physical environment on the scale of organisms and replicate those conditions in laboratory experiments, I will use examples from our studies of swimming and crawling by microscopic larvae of bottom-dwelling marine animals in turbulent, wave-driven ambient flow (Koehl and Reidenbach, 2008). Some zooplankton are abundant and large enough that their swimming relative to the water in which they are being carried can be measured using PIV and trajectory tracking simultaneously in the field (Sutherland et al., 2011). In other cases, the organisms are too rare or small to be studied in the field, so we turn to the lab.

We used the sea slug *Phestilla sibogae*, whose larvae recruit onto coral reefs, and the tube worm *Hydroides elegans*, whose larvae recruit onto fouling communities in harbors, to study how larvae carried in ambient flow can land and stay on suitable surfaces. During different seasons and times of day, we measured the velocity of the wavy, turbulent water flow in the field at different distances from surfaces of coral reefs (Fig. 1A) and fouling communities, and used spectra of these flow records (Fig. 1B) to recreate the same velocity profiles and fluctuations over coral reefs or fouling communities in laboratory wave-flumes (Reidenbach et al., 2009; Koehl et al., 2013; Pepper et al., 2015). By illuminating a millimeter-thick slice of moving water in the flume with a sheet of laser light and making high-speed videos of marker particles and of fluorescent dye (simulating odors) leaching from the reef or fouling community, we could simultaneously use PIV and planar laser-induced fluorescence (PLIF) to measure instantaneous fine-scale distributions of velocities and odors in the water (Fig. 3A,B). We used laser Doppler velocimetry (LDV) to measure velocity within a few hundred micrometers from surfaces of coral reefs (Fig. 2A) or fouling communities to determine water motion encountered by microscopic larvae near and on those surfaces (Reidenbach et al., 2009; Koehl et al., 2013). LDV can resolve flow microhabitats produced by tiny topographic features (<1 mm).

Using agent-based models of larvae swimming in our PIV–PLIF data, we determined how their trajectories were affected by their motion through the water, rotation by local shear, response to odors and transport by ambient flow (Koehl et al., 2007; Koehl and Cooper, 2015). Following calculated trajectories of larvae through our PIV–PLIF data, we determined the temporal patterns of their encounters with odors from the substratum (Koehl et al., 2007;

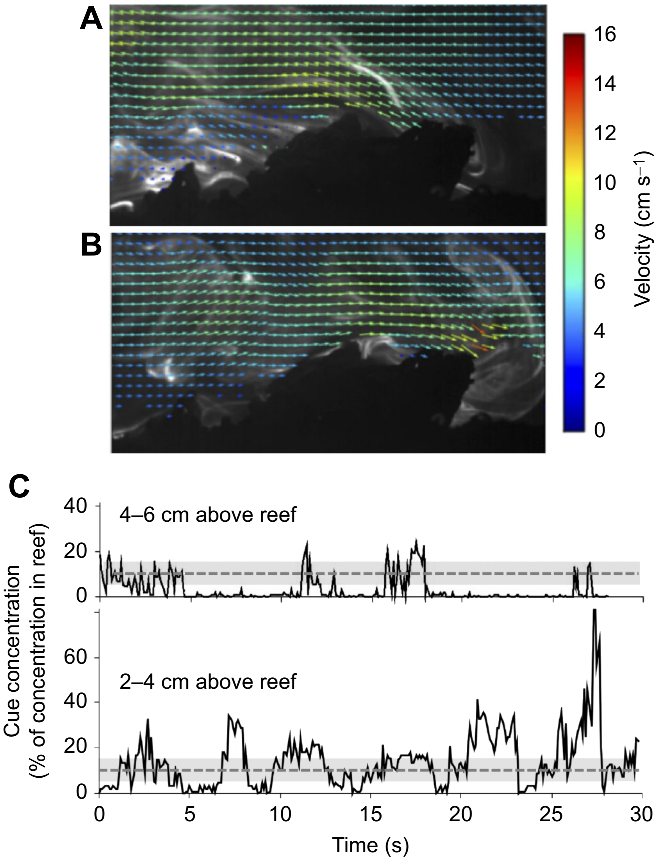

**Fig. 3. Velocity vectors and concentrations of chemical cues in the water above benthic communities in wavy water flow.** (A,B) Maps at different instants of velocity vectors and concentrations of chemical cues released from a fouling community (concentration proportional to pixel brightness) in a wave flume. (C) Concentration of a chemical cue released from corals that are encountered by a larva of *P. sibogae* swimming at different heights above the reef (calculated as described in Koehl et al., 2007). Dashed lines indicate the mean threshold concentration of cue that stimulated larvae to sink (gray shading indicates standard deviation) (Hadfield and Koehl, 2004). The frequency of encounters with odor filaments above threshold concentration increases as larvae get closer to the reef.

Koehl and Cooper, 2015). It was thought that larvae encounter a diffuse concentration gradient of chemical signals above a benthic community (Eckman et al., 1994), but we discovered that larvae swim through fine filaments of odor, and that the frequency of those encounters increases as larvae near the substratum (Fig. 3C). Using this information, we designed a device to video responses of *P. sibogae* larvae swimming through fine filaments of coral odor at realistic concentrations and temporal patterns (Hadfield and Koehl, 2004). These experiments revealed that these larvae sink in odor filaments above a threshold concentration, and resume swimming after exiting such filaments. Giving larvae this behavior in our agent-based models revealed that this simple on–off behavior enhanced rates of larval settlement onto a reef by ∼20% (Koehl et al., 2007). We tested our model in the field by using it to predict the spatial distribution of *P. sibogae* landing on coral reefs, and found that field recruitment patterns matched model predictions (Hadfield et al., 2006). The frequency of encounters with pulses of high shear, vorticity and acceleration also increases as larvae get closer to surfaces (Koehl and Cooper, 2015; Pepper et al., 2015). We are currently using fluidic devices to mimic the temporal patterns of these hydrodynamic perturbations so we can record larval responses through a microscope.

LDV measurements of velocity along surfaces enabled us to study swimming and crawling of microscopic organisms near or on test surfaces in realistic flow. We investigated reactions of *H. elegans* larvae to surfaces of developing fouling communities by mimicking LDV-measured flow in a miniflume small enough for microvideography. PIV and larval tracking revealed that larvae swimming within millimeters of a surface are rotated by the local shear such that they 'bounce' along the substratum, which enhances their exploration of surfaces (Koehl et al., 2022). LDV data also enabled ecologically relevant measurements of larval adhesive strength. Standard procedure for measuring adhesive strength of microorganisms is to expose surfaces where they are attached to steady water flows of different velocities to determine the shear stress required to dislodge them (e.g. Koehl and Hadfield, 2004). However, flow on larvae on surfaces is pulsatile (Fig. 2A), so we developed a device to expose larvae on surfaces to pulses of flow mimicking those they encounter in nature (Fig. 2B). *Phestilla sibogae* adhere with mucus, a shear-thinning material that behaves like an elastic solid until it is sheared beyond a critical strain, at which point it becomes a viscous liquid (Denny, 1984). The mucus attaching larvae exposed to steady water motion is deformed far enough to flow and larvae are sheared off surfaces, but in brief pulses of water motion the mucus acts like an elastic bungie cord that stretches and then recoils before the next pulse. The adhesive strength of larvae exposed to realistic pulses of water motion revealed that they are washed away from the tips of coral branches, but can adhere to surfaces in the slower flow within the reef (Fig. 2A).

## Mechanical ecology and evolutionary biology

Arnold (1983) formalized a framework for studying the evolution of morphology: structure determines organism performance, which in turn affects fitness (Fig. 4). Comparative biomechanics, which discovers how morphology affects aspects of performance, has enhanced our understanding of evolution in several ways. The non-linear dependence of performance on dimensions of structures reveals regions of morphospace where there is permission for diversity of form without functional consequences and areas where small structural changes have large effects on performance or enable

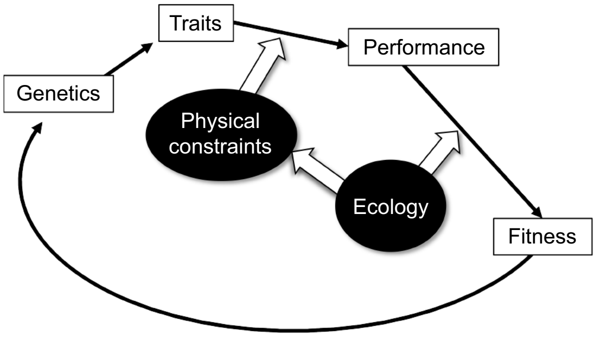

**Fig. 4. Diagram of Arnold's framework for the evolution of morphology.** The structure of various traits affects their performance, which in turn affects the fitness of the organisms with those traits. The relative fitness of different individuals determines the prevalence of different genotypes in the population, which determines the morphologies of traits in that population (Arnold, 1983). Here, I argue that physical constraints limit biomechanical performance, and that ecology determines how performance affects fitness, but can also influence how physical constraints affect performance.

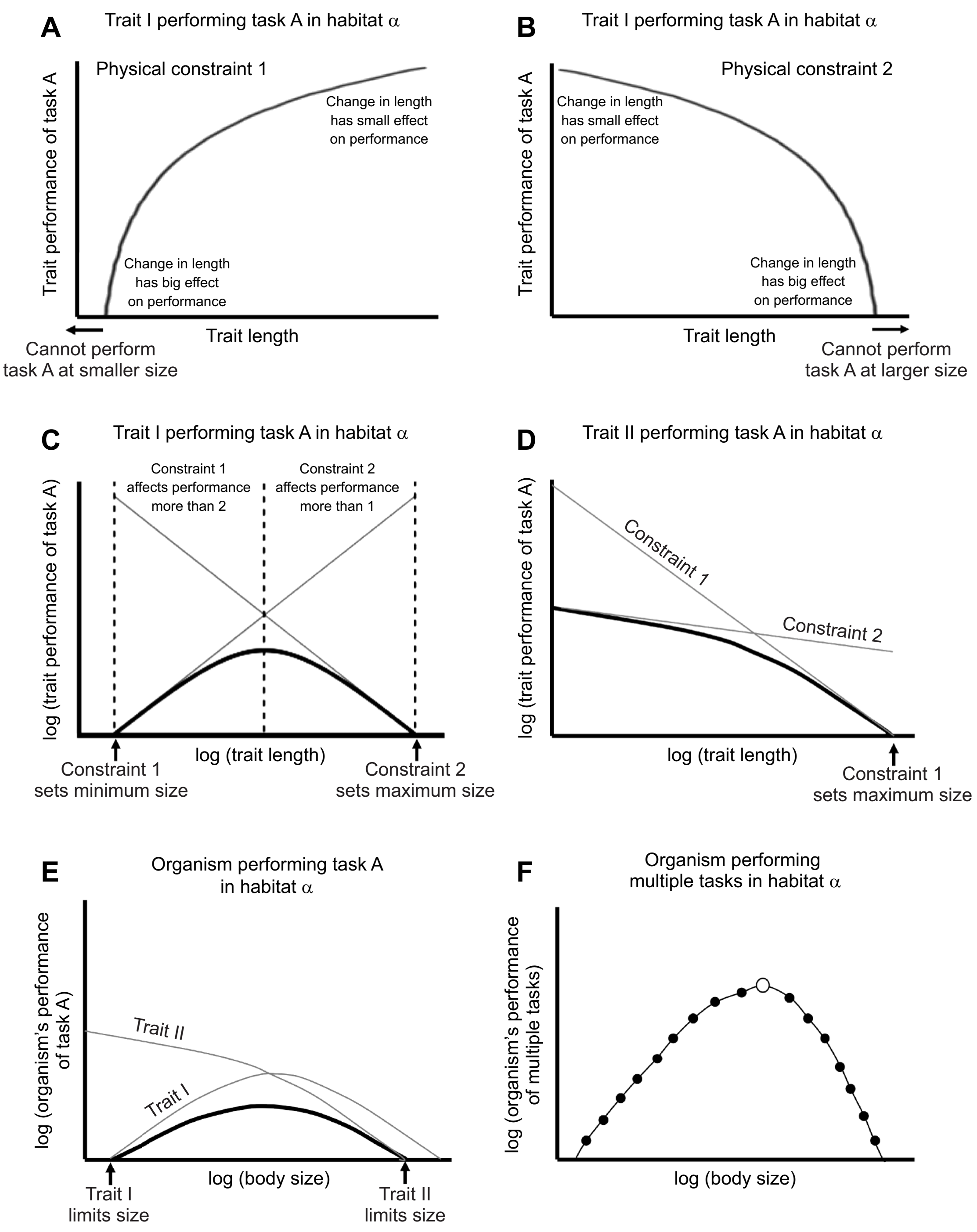

**Fig. 5. Using mechanical ecology to study the evolution of morphology.** Diagrams of the basic approach of Kempes et al. (2019), where the mathematics of this approach are described. (A,B) Determine how different physical constraints in a specific type of habitat affect performance of a defined task for a range of lengths of a body part (Trait I). These examples show different non-linear effects on performance by constraints 1 and 2. (C) Calculate net performance of a task as a function of trait length due to multiple constraints acting simultaneously. In this example, constraint 1 has a bigger effect on performance when the trait is short, and constraint 2 is more important when the trait is long. (D) Several traits can affect the performance of a task. In this example, physical constraints 1 and 2 have different effects on task performance as a function of length for Trait II than they do for Trait I. (E) Calculate net performance by the organism of a task carried out by multiple traits acting together. (F) Organisms perform multiple tasks (e.g. run, chew), each depending on multiple traits. Overall performance of the organism (a measure of an ecologically important function such as prey capture per energy expended, or a measure of fitness such as lifetime reproductive output) is the net result of many tasks. In this example, physical constraints limit body size; the black circles indicate the peak performance possible for different body sizes, and the white circle indicates the optimal body size where overall performance is maximized. These steps can be repeated for a different type of habitat because environment can affect biomechanical performance.

novel functions (Fig. 5A,B) (Koehl, 1996). These physical rules, along with analyses of how multiple morphological features affect the performance of specific tasks ('many-to-one mapping') provide insights about the evolution of functional innovations (Koehl, 2000; Wainwright, 2007). Many studies published in JEB have mapped biomechanical function onto a phylogeny to reveal the evolutionary history of functional traits in a clade (reviewed in Wainwright and Reilly, 1994; Bels et al., 2003; Müller, 2003; Wainwright, 2007; Patek and Longo, 2018). Physical and mathematical models of biomechanical function of extinct organisms can shed light on the history of life on Earth (Kingsolver and Koehl, 1985; Alexander, 2003a,b; Koehl, 2003).

Traditionally, ecology entered into evolutionary analyses because it determines how performance translates into fitness, but studies of mechanical ecology reveal that the environment also influences how morphology affects performance (Fig. 4). Two recent papers have proposed quantitative approaches for incorporating mechanical ecology into evolutionary biology (Kempes et al., 2019; Higham et al., 2021). Both recognize that physical laws set limits on biological form, that trade-offs between different functions affect overall performance, that different structures and mechanisms can accomplish a given function, that ecological conditions affecting performance and fitness vary in space and time, and that ontogenetic changes of organisms are important. Higham et al. (2021) use safety factor as a key metric in assessing the evolution of form and biomechanical performance, whereas Kempes et al. (2019) consider the interactions of multiple tasks in determining overall organism performance and physical limits (approach summarized in Fig. 5).

## Conclusions

The diverse examples described above show that the physical environment and ecological interactions of organisms can determine how their morphology affects biomechanical functions that can impact their fitness. Therefore, field studies of how organisms function in their variable natural habitats throughout their ontogeny help us understand ecologically relevant biomechanical performance and the evolution of morphology. If we can couple an organism's corpse (morphology only) and ghost (functional traits only, without underlying morphology), and connect them with its ecology, then our understanding of its biomechanical design will not be a mirage.

### Acknowledgements

I salute mentors who taught me about biomechanics, ecology and critical quantitative thinking: Steve Wainwright, Steve Vogel, Bob Paine, Richard Strathmann, John Currey and George Oster. I thank students, postdocs and collaborators who worked with me and stimulated me to explore new areas. I am grateful for grants from the National Science Foundation and Office of Naval Research, and for a MacArthur Fellowship, which supported my research cited here.

### Competing interests

The author declares no competing or financial interests.

### Funding

My research cited here was supported by the National Science Foundation, Office of Naval Research, and a MacArthur Fellowship. My funding while writing this paper was National Science Foundation grants DMS-2054143 and IOS-2136019.

### References

**Ahmed, I. and Faruque, I. A.** (2022). High Speed Visual Insect Swarm Tracker (Hi-VISTA) used to identify the effects of confinement on individual insect flight. *Bioinsp. Biomim.* **17**, 046012. doi:10.1088/1748-3190/ac6849

**Alexander, D. E.** (2004). *Nature's Flyers: Birds, Insects, and the Biomechanics of Flight*. Baltimore, MD: Johns Hopkins University Press.

**Alexander, R. McN.** (1968). *Animal Mechanics.* London, UK: Sidgwick and Jackson.

**Alexander, R. McN.** (1984). Elastic energy stores in running vertebrates. *Am. Zool.* **24**, 85-94. doi:10.1093/icb/24.1.85

**Alexander, R. McN.** (1981). Factors of safety in the structure of animals. *Sci. Prog.* **67**, 109-130.

**Alexander, R. McN.** (2002). Energetics and optimization of human walking and running: The 2000 Raymond Pearl memorial lecture. *Am. J. Human Biol.* **14**, 641-648. doi:10.1002/ajhb.10067

**Alexander, R. McN.** (2003a). *Principles of Animal Locomotion.* Princeton, NJ: Princeton University Press.

**Alexander, R. McN.** (2003b). Achievements and limitations in the mechanics of extinct organisms. In *Vertebrate Biomechanics and Evolution* (ed. V. L. Bels, J. P. Gasc,and A. Casios), pp. 11-22. Oxford, UK: BIOS Scientific Publishers Ltd.

**Alexander, R. M. and Jayes, A. S.** (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool.* **201**, 135-152. doi:10.1111/j.1469-7998.1983.tb04266.x

**Altshuler, D. L., Dickson, W. B., Vance, J. T., Roberts, S. P. P. and Dickinson, M. H.** (2005). Short-amplitude high-frequency wing strokes determine the aerodynamics of honeybee flight. *Proc. Natl. Acad. Sci. USA* **102**, 18213-18218. doi:10.1073/pnas.0506590102

**Arnold, S. J.** (1983). Morphology, performance, and fitness. *Am. Zool.* **23**, 347-361. doi:10.1093/icb/23.2.347

**Baskett, M. L.** (2012). Integrating mechanistic organism–environment interactions into the basic theory of community and evolutionary ecology. *J. Exp. Biol.* **215**, 948-961. doi:10.1242/jeb.059022

**Bauer, U., Poppinga, S. and Müller, U. K.** (2020). Mechanical ecology: taking biomechanics to the field. *Integr. Comp. Biol.* **60**, 820-828. doi:10.1093/icb/icaa018

**Bell, E. C. and Denny, M. W.** (1994). Quantifying "wave exposure": a simple device for recording maximum velocity and results of its use at several field sites. *J. Exp. Mar. Biol. Ecol.* **181**, 9-29. doi:10.1016/0022-0981(94)90101-5

**Bell, E. C. and Gosline, J. M.** (1997). Strategies for life in flow: tenacity, morphometry, and probability of dislodgment of two *Mytilus* species. *Mar. Ecol. Prog. Ser.* **159**, 197-208. doi:10.3354/meps159197

**Bels, V. L., Gasc, J. P. and Casinos, A.** (2003). *Vertebrate Biomechanics and Evolution*. Oxford, UK: BIOS Scientific Publishers Ltd.

**Black, R.** (1976). The effects of grazing by the limpet, *Acmaea insessa*, on the kelp, *Egregia laevigata*, in the intertidal zone. *Ecology* **57**, 265-277. doi:10.2307/1934815

**Blickham, R. and Full, R. J.** (1993). Similarity in multilegged locomotion: bouncing like a monopode. *J. comp. Physiol.* **173**, 509-517.

**Boulding, E. G.** (1984). Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *J. Exp. Mar. Biol. Ecol.* **76**, 201-223. doi:10.1016/0022-0981(84)90189-8

**Browning, R. C., Modica, J. R., Kram, R. and Goswami, A.** (2007). The effects of adding mass to the legs on the energetics and biomechanics of walking. *Med. Sci. Sports Exerc.* **39**, 515-525. doi:10.1249/mss.0b013e31802b3562

**Burnett, N. P. and Gaylord, B.** (2022). Flow, form, and force: methods and frameworks for field studies of macroalgal biomechanics. *J. Exp. Bot.* **73**, 1122-1138. doi:10.1093/jxb/erab498

**Burnett, N. P. and Koehl, M. A. R.** (2019). Mechanical properties of the wave-swept kelp *Egregia menziesii* change with season, growth rate and herbivore wounds. *J. Exp. Biol.* **222**, jeb190595. doi:10.1242/jeb.190595

**Burnett, N. P. and Koehl, M. A. R.** (2020). Thallus pruning does not enhance survival or growth of a wave-swept kelp. *Mar. Biol.* **167**, 52. doi:10.1007/s00227-020-3663-5

**Burnett, N. P. and Koehl, M. A. R.** (2021). Age affects the strain–rate dependence of mechanical properties of kelp tissues. *Am. J. Bot.* **108**, 769-776. doi:10.1002/ajb2.1662

**Burnett, N. P. and Koehl, M. A. R.** (2022). Ecological biomechanics of damage to macroalgae. *Front. Plant Sci.* **13**, 981904. doi:10.3389/fpls.2022.981904

**Burnett, N. P., Badger, M. A. and Combes, S. A.** (2020). Wind and obstacle motion affect honeybee flight strategies in cluttered environments. *J. Exp. Biol.* **223**, jeb222471. doi:10.1242/jeb.222471

**Campbell, G. S. and Norman, J.** (1998). *An Introduction to Environmental Biophysics*, 2nd edn. New York: Springer.

**Carrington, E.** (1990). Drag and dislodgment of an intertidal macroalga: Consequences of morphological variation in Mastocarpus papillatus Kützing. *J. Exp. Mar. Biol. Ecol.* **139**, 185-200. doi:10.1016/0022-0981(90)90146-4

**Carrington, E.** (2002). Seasonal variation in the attachment strength of blue mussels: causes and consequences. *Limnol. Oceanog.* **47**, 1723-1733. doi:10.4319/lo.2002.47.6.1723

**Carrington, E. and Gosline, J. M.** (2004). Mechanical design of mussel byssus: Load cycle and strain rate dependence. *Am. Malacol. Bull.* **18**, 135-142.

**Catton, K. B., Webster, D. R., Kawaguchi, S. and Yen, J.** (2011). The hydrodynamic disturbances of two species of krill: implications for aggregation structure. *J. Exp. Biol.* **214**, 1845-1856. doi:10.1242/jeb.050997

**Cheer, A. Y. L. and Koehl, M. A. R.** (1987). Paddles and rakes: Fluid flow through bristled appendages of small organisms. *J. Theor. Biol.* **129**, 17-39. doi:10.1016/S0022-5193(87)80201-1

**Clemo, W. C., Giles, K. D. and Dorgan, K. M.** (2022). Biological influences on coastal muddy sediment structure following resuspension. *Limnol. Oceanog.* **67**, 2466-2482. doi:10.1002/lno.12213

**Coelho, J. R. and Hoagland, J.** (1995). Load-lifting capacities of three species of yellowjackets (*Vespula*) foraging on honey-bee corpses. *Funct. Ecol.* **9**, 171-174. doi:10.2307/2390561

**Combes, S. A. and Dudley, R.** (2009). Turbulence-driven instabilities limit insect flight performance. *Proc. Nat.l Acad. of Sci. USA* **106**, 9105-9108. doi:10.1073/pnas.0902186106

**Crall, J. D., Ravi, S., Mountcastle, A. M. and Combes, S. A.** (2015). Bumblebee flight performance in cluttered environments: Effects of obstacle orientation, body size and acceleration. *J. Exp. Biol.* **218**, 2728-2737. doi:10.1242/jeb.121293

**Crall, J. D., Chang, J. J., Oppenheimer, R. L. and Combes, S. A.** (2017). Foraging in an unsteady world: Bumblebee flight performance in field-realistic turbulence. *Interface Focus* **7**, 20160086. doi:10.1098/rsfs.2016.0086

**Currey, J. D. and Taylor, J. D.** (1974). The mechanical behaviour of some molluscan hard tissues. *J. Zool.* **173**, 395-406. doi:10.1111/j.1469-7998.1974.tb04122.x

**Dabiri, J. O.** (2010). Role of vertical migration in biogenic ocean mixing. *Geophys. Res. Lett.* **37**, L11602. doi:10.1029/2010GL043556

**Daniel, T. L. and Meyhofer, E.** (1989). Size limits in escape locomotion of carridean shrimp. *J. Exp. Biology* **143**, 245-265. doi:10.1242/jeb.143.1.245

**Denny, M. W.** (1982). Forces on intertidal organisms due to breaking ocean waves: Design and application of a telemetry system. *Limnol. Oceanog.* **27**, 178-183. doi:10.4319/lo.1982.27.1.0178

**Denny, M. W.** (1984). Mechanical properties of pedal mucus and their consequences for gastropod structure and performance. *Am. Zool.* **24**, 23-36. doi:10.1093/icb/24.1.23

**Denny, M.** (2012). Editorial: Biophysics, bioenergetics and mechanistic approaches to ecology. *J. Exp. Biol.* **215**, 871. doi:10.1242/jeb.069575

**Denny, M.** (2016). *Ecological Mechanics: Principles of Life's Physical Interactions*. Princeton, NJ: Princeton University Press.

**Denny, M. W. and Dowd, W.** (2012). Biophysics, environmental stochasticity, and the evolution of thermal safety margins in intertidal limpets. *J. Exp. Biol.* **215**, 934-947. doi:10.1242/jeb.058958

**Denny, M. W. and Gaylord, B.** (2010). Marine ecomechanics. *Ann. Rev. Mar. Sci.* **2**, 89-114. doi:10.1146/annurev-marine-120308-081011

**Denny, M. W. and Wethey, D.** (2001). Physical processes that generate patterns in marine communities. In *Marine Community Ecology* (ed. M. Bertness, M. Hay and S. Gaines), pp. 3-37. New York: Sinauer Press.

**Denny, M. W., Hunt, L. J., Miller, L. P. and Harley, C. D.** (2009). On the prediction of extreme ecological events. *Ecol. Monogr.* **79**, 397-421. doi:10.1890/08-0579.1

**Denny, M. W., Helmuth, B., Leonard, G. H., Harley, C. D., Hunt, L. J. and Nelson, E. K.** (2004). Quantifying scale in ecology: lessons from a wave–swept shore. *Ecol. Monog.* **74**, 513-532. doi:10.1890/03-4043

**Dillon, M. and Dudley, R.** (2004). Allometry of maximum vertical force production during hovering flight of neotropical orchid bees (Apidae, Euglossini). *J. Exp. Biol.* **207**, 417-425. doi:10.1242/jeb.00777

**Domenici, P.** (2003). Habitat, body design and the swimming performance of fish. In *Vertebrate Biomechanics and Evolution* (ed. V. L. Bels, J. P. Gasc and A. Casios), pp. 137-160. Oxford, UK: BIOS Scientific Publishers Ltd.

**Eckman, J. E.** (1985). Flow disruption by an animal-tube mimic affects sediment bacterial colonization. *J. Mar. Res.* **43**, 419-435. doi:10.1357/002224085788438685

**Eckman, J. E., Werner, F. E. and Gross, T. F.** (1994). Modeling some effects of behavior on larval settlement in a turbulent boundary layer. *Deep-Sea Res II* **41**, 185-208. doi:10.1016/0967-0645(94)90067-1

**Edlund, A. F. and Koehl, M. A. R.** (1998). Adhesion and reattachment of compound ascidians to various substrata. *J. Exp. Biol.* **201**, 2397-2402. doi:10.1242/jeb.201.16.2397

**Emerson, S. B. and Koehl, M. A. R.** (1990). The interaction of behavior and morphology in the evolution of a novel locomotor type: "Flying frogs". *Evolution* **44**, 1931-1946.

**Evangelista, D., Cardona, G., Guenther-Gleason, E., Huynh, T., Kwong, A., Marks, D., Ray, N., Tisbe, A., Tse, K. and Koeh, M. A. R.** (2014). Aerodynamic characteristics of a feathered dinosaur measured using physical models. I. Effects of form on static stability and control effectiveness. *PLOS One* **9**, e85203. doi:10.1371/journal.pone.0085203

**Fonseca, M. S., Fourqurean, J. W. and Koehl, M. A. R.** (2019). Effect of seagrass on current speed: importance of flexibility versus shoot density. *Front. Mar. Sci.* **6**, 376. doi:10.3389/fmars.2019.00376

**Gates, D. M.** (1975). Introduction: Biophysical ecology. In *Perspectives of Biophysical Ecology* (ed. D. M. Gates and R. B. Schmerl), pp. 1-28. New York: Springer Verlag.

**Gates, D. M.** (1980). *Biophysical Ecology.* New York: Springer Verlag.

**Gaylord, B.** (2000). Biological implications of surf–zone flow complexity. *Limnol. Oceanog.* **45**, 174-188. doi:10.4319/lo.2000.45.1.0174

**Gaylord, B., Denny, M. W. and Koehl, M. A. R.** (2003). Modulation of wave forces on kelp canopies by alongshore currents. *Limnol. Oceanog.* **48**, 860-871. doi:10.4319/lo.2003.48.2.0860

**Gaylord, B., Nickols, K. J. and Jurgens, L.** (2012). Roles of transport and mixing processes in kelp forest ecology. *J. Exp. Biol.* **215**, 997-1007. doi:10.1242/jeb.059824

**Greene, H. W.** (1994). Systematics and natural history: Foundations for understanding and conserving biodiversity. *Am. Zool.* **34**, 48-56. doi:10.1093/icb/34.1.48

**Hadfield, M. G. and Koehl, M. A. R.** (2004). Rapid behavioral responses of an invertebrate larva to dissolved settlement cue. *Biol. Bull.* **207**, 28-43. doi:10.2307/1543626

**Hadfield, M. G., Faucci, A. and Koehl, M. A. R.** (2006). Measuring recruitment of minute larvae in a complex field environment: The corallivorous nudibranch *Phestilla sibogae* (Bergh). *J. Exp. Mar. Biol. Ecol.* **338**, 57-72. doi:10.1016/j.jembe.2006.06.034

**Hambly, C., Harper, E. J. and Speakman, J. R.** (2004). The energy cost of loaded flight is substantially lower than expected due to alterations in flight kinematics. *J. Exp. Biol.* **207**, 3969-3976. doi:10.1242/jeb.01234

**Harwell, M. C. and Orth, R. J.** (2002). Long-distance dispersal potential in a marine macrophyte. *Ecology* **83**, 3319-3330. doi:10.1890/0012-9658(2002)083[3319:LDDPIA]2.0.CO;2

**Helmuth, B., Broitman, B. R., Yamane, L., Gilman, S. E., Mach, K., Mislan, K. A. and Denny, M. W.** (2010). Organismal climatology: analyzing environmental variability at scales relevant to physiological stress. *J. Exp. Biol.* **213**, 995-1003. doi:10.1242/jeb.038463

**Holbrook, N. M., Denny, M. and Koehl, M. A. R.** (1991). Intertidal "trees": Consequences of aggregation on the mechanical and photosynthetic characteristics of sea palms. *J. Exp. Mar. Biol. Ecol.* **146**, 39-67. doi:10.1016/0022-0981(91)90254-T

**Herrel, A., Speck, T. and Rowe, N. P.** (eds) (2006). *Ecology and Biomechanics – A Mechanical Approach to the Ecology of Animals and Plants*. Boca Raton, FL: CRC Press.

**Higham, T. E., Ferry, L. A., Schmitz, L., Irschick, D. J., Starko, S., Anderson, P. S., Bergmann, P. J., Jamniczky, H. A., Monteiro, L. R., Navon, D. et al.** (2021). Linking ecomechanical models and functional traits to understand phenotypic diversity. *Trends Ecol. Evol.,* **36**, 860-873. doi:10.1016/j.tree.2021.05.009

**Huang, T. W. P., Kuo, A. D.** (2014). Mechanics and energetics of load carriage during human walking. *J. Exp. Biol.* **21**, 605-613. doi:10.1242/jeb.091587

**Jackson, G. A. and Winant, C. D.** (1983). Effect of a kelp forest on coastal currents. *Cont. Shelf Res.* **2**, 75-80. doi:10.1016/0278-4343(83)90023-7

**Jagnandan, K. and Higham, T. E.** (2018). How rapid changes in body mass affect the locomotion of terrestrial vertebrates: Ecology, evolution, and biomechanics of a natural perturbation. *Biol. J. Linn. Soc.* **124**, 279-293. doi:10.1093/biolinnean/bly056

**Jayaram, K. and Full, R. J.** (2016). Cockroaches traverse crevices, crawl rapidly in confined spaces, and inspire a soft, legged robot. *Proc. Nat. Acad. Sci. USA* **113**, E950-E957. doi:10.1073/pnas.1514591113

**Jindrich, D. L. and Full, R. J.** (2002). Dynamic stabilization of rapid hexapedal locomotion. *J. Exp. Biol.* **205**, 2810-2823. doi:10.1242/jeb.205.18.2803

**Johnson, A. S.** (1990). Flow around phoronids: Consequences of a neighbor to suspension feeders. *Limnol. Oceanogr.* **35**, 1395-1401. doi:10.4319/lo.1990.35.6.1395

**Johnson, A. J. and Koehl, M. A. R.** (1994). Maintenance of dynamic strain similarity and environmental stress factor in different flow habitats: Thallus allometry and material properties of a giant kelp. *J. Exp. Biol.* **195**, 381-410. doi:10.1242/jeb.195.1.381

**Jumars, P. W.** (1993). *Concepts in Biological Oceanography: An Interdisciplinary Primer*. New York: Oxford University Press.

**Jumars, P. A. and Nowell, A. R.** (1984). Fluid and sediment dynamic effects on marine benthic community structure. *Am. Zool.* **24**, 45-55. doi:10.1093/icb/24.1.45

**Källströma, B., Nyqvist, A., Abergb, P., Bodinb, M. and Andrea, C.** (2008). Seed rafting as a dispersal strategy for eelgrass (*Zostera marina*). *Aquat. Bot.* **88**, 148-153. doi:10.1016/j.aquabot.2007.09.005

**Katija, K.** (2012). Biogenic inputs to ocean mixing. *J. Exp. Biol.* **215**, 1040-1049. doi:10.1242/jeb.059279

**Katija, K. and Dabiri, J. O.** (2008). In situ field measurements of aquatic animal-fluid interactions using a self-contained underwater velocimetry apparatus (SCUVA). *Limnol. Oceanogr. Methods* **6**, 162-171. doi:10.4319/lom.2008.6.162

**Kawai, S.** (1981). Visualization of airflow separation over wind-wave crests under moderate wind. *Boundary-Layer Meteorol.* **21**, 93-104. doi:10.1007/BF00119370

**Kempes, C. P., Koehl, M. A. R. and West, G. B.** (2019). The scales that limit: The physical boundaries of evolution. *Front. Ecol. Evol.* **7**, 242. doi:10.3389/fevo.2019.00242

**Kingsolver, J. G. and Koehl, M. A. R.** (1985). Aerodynamics, thermoregulation, and the evolution of insect wings: Differential scaling and evolutionary change. *Evolution* **39**, 488-504. doi:10.1111/j.1558-5646.1985.tb00390.x

**Kiørboe, T., Visser, A. and Andersen, K. H.** (2018). A trait-based approach to ocean ecology. *ICES J. Mar. Sci.* **75**, 1849-1863. doi:10.1093/icesjms/fsy090

**Knight, K.** (2012). Biophysics, bioenergetics and mechanistic approaches to ecology. *J. Exp. Biol.* **215**, i-iii. doi:10.1242/jeb.082024

**Koch, E. W., Ackerman, J. D., Verduin, J. and van Keulen, M.** (2006). Fluid dynamics in seagrass ecology - from molecules to ecosystems. In *Seagrasses: Biology, Ecology and Conservation* (ed. A. W. D. Larkum, C. M. Duarte and R. J. Orth), pp. 193-225. Dordrecht: Springer.

**Koehl, M. A. R.** (1976). Mechanical design in sea anemones. In *Coelenterate Ecology and Behavior* (ed. G. O. Mackie), pp. 23-31. Boston, MA: Springer.

**Koehl, M. A. R.** (1977a). Effects of sea anemones on the flow forces they encounter. *J. Exp. Biol.* **69**, 87-105. doi:10.1242/jeb.69.1.87

**Koehl, M. A. R.** (1977b). Mechanical diversity of the connective tissue of the body wall of sea anemones. *J. Exp. Biol.* **69**, 107-125. doi:10.1242/jeb.69.1.107

**Koehl, M. A. R.** (1977c). Mechanical organization of cantilever-like sessile organisms: Sea anemones. *J. Exp. Biol.* **69**, 127-142. doi:10.1242/jeb.69.1.127

**Koehl, M. A. R.** (1977d). Water flow and the morphology of zoanthid colonies. *Proc. Third Int. Coral Reef Symp.* **1**, 437-444.

**Koehl, M. A. R.** (1982). The interaction of moving water and sessile organisms. *Sci. Am.* **247**, 124-132. doi:10.1038/scientificamerican1282-124

**Koehl, M. A. R.** (1984). How do benthic organisms withstand moving water? *Am. Zool.* **24**, 57-70. doi:10.1093/icb/24.1.57

**Koehl, M. A. R.** (1989). From individuals to populations. In *Perspectives in Ecological Theory* (ed. R. M. May, J. Roughgarden and S. A. Levin), pp. 39-53. Princeton, NJ: Princeton University Press.

**Koehl, M. A. R.** (1992). Hairy little legs: Feeding, smelling, and swimming at low Reynolds number. *Contemp. Math.* **141**, 33-64. doi:10.1090/conm/141/02

**Koehl, M. A. R.** (1995). Fluid flow through hair-bearing appendages: Feeding, smelling, and swimming at low and intermediate Reynolds numbers. *Soc. Exp. Biol. Symp.* 49, 157-182.

**Koehl, M. A. R.** (1996). When does morphology matter? *Ann. Rev. Ecol. Syst.* **27**, 501-542. doi:10.1146/annurev.ecolsys.27.1.501

**Koehl, M. A. R.** (1999). Ecological biomechanics: life history, mechanical design, and temporal patterns of mechanical stress. *J. Exp. Biol.* **202**, 3469-3476. doi:10.1242/jeb.202.23.3469

**Koehl, M. A. R.** (2000). Consequences of size change during ontogeny and evolution. In *Scaling in Biology* (ed. J. H. Brown and G. B. West), pp. 67-86. New York: Oxford University Press.

**Koehl, M. A. R.** (2003). Physical modelling in biomechanics. *Phil Trans. Roy. Soc. Lond. B* **358**, 1589-1596. doi:10.1098/rstb.2003.1350

**Koehl, M. A. R.** (2004). Biomechanics of microscopic appendages: Functional shifts caused by changes in speed. *J. Biomech.* **37**, 789-795. doi:10.1016/j.jbiomech.2003.06.001

**Koehl, M. A. R.** (2010). How does morphology affect performance in variable environments? In *In Search of the Causes of Evolution. From Field Observations to Mechanisms* (ed. P.R. Grant and B. Grant), pp. 177-191. Princeton, NJ: Princeton University Press.

**Koehl, M. A. R.** (2022). Ecological biomechanics of marine macrophytes. *J. Exp. Bot.* **73**, 1104-1121. doi:10.1093/jxb/erab536

**Koehl, M. A. R. and Alberte, R. S.** (1988). Flow, flapping, and photosynthesis of macroalgae: Functional consequences of undulate blade morphology. *Mar. Biol.* **99**, 435-444. doi:10.1007/BF02112137

**Koehl, M. A. R. and Cooper, T.** (2015). Swimming in an unsteady world. *Integr. Comp. Biol.* **55**, 683-697. doi:10.1093/icb/icv092

**Koehl, M. A. R. and Daniel, T. L.** (2022). Hydrodynamic interactions between macroalgae and their epibionts. *Front. Mar. Sci.* **9**, 872960. doi:10.3389/fmars.2022.872960

**Koehl, M. A. R. and Hadfield, M. G.** (2004). Soluble settlement cue in slowly-moving water within coral reefs induces larval adhesion to surfaces. *J. Mar. Syst.* **49**, 75-88. doi:10.1016/j.jmarsys.2003.06.003

**Koehl, M. A. R. and Reidenbach, M. A.** (2008). Swimming by microscopic organisms in ambient water flow. *Exp. Fluids* **43**, 755-768. doi:10.1007/s00348-007-0371-6

**Koehl, M. A. R. and Silk, W. K.** (2021). How kelp in drag lose their ruffles: Environmental cues, growth kinematics, and mechanical constraints govern curvature. *J. Exp. Bot.* **72**, 3677-3687. doi:10.1093/jxb/erab111

**Koehl, M. A. R. and Wainwright, S. A.** (1977). Mechanical adaptations of a giant kelp. *Limnol. Oceanogr.* **22**, 1067-1071. doi:10.4319/lo.1977.22.6.1067

**Koehl, M. A. R. and Wolcott, B. D.** (2004). Can function at the organismal level explain ecological patterns? *Ecology* **85**, 1808-1810. doi:10.1890/03-0756

**Koehl, M. A. R., Powell, T. M. and 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, T. M. Powell and S. A. Levin), pp. 50-60. Berlin: Springer.

**Koehl, M. A. R., Powell, T. M. and Dobbins, E. L.** (1997). Effects of algal turf on mass transport and flow microhabitat of ascidians in a coral reef lagoon. *Proc. 8th Int. Coral Reef Symp.* **2**, 1087-1092.

**Koehl, M. A. R., Koseff, J. R., Crimaldi, J. P., McCay, M. G., Cooper, T., Wiley, M. B. and Moore, P. A.** (2001). Lobster sniffing: Antennule design and hydrodynamic filtering of information in an odor plume. *Science.* **294**, 1948-1951. doi:10.1126/science.1063724

**Koehl, M. A. R., Strother, J. A., Reidenbach, M. A., Koseff, J. R. and Hadfield, M. G.** (2007). Individual-based model of larval transport to coral reefs in turbulent, wave-driven flow: Effects of behavioral responses to dissolved settlement cues. *Mar. Ecol Prog. Ser.* **335**, 1-18. doi:10.3354/meps335001

**Koehl, M. A. R., Evangelista, D. and Yang, K.** (2011). Using physical models to study the gliding performance of extinct animals. *Integr. Comp. Biol.* **51**, 1002-1018. doi:10.1093/icb/icr112

**Koehl, M. A. R., Crimaldi, J. P. and Dombroski, D. E.** (2013). Wind chop and ship wakes determine hydrodynamic stresses on larvae settling on different microhabitats in fouling communities. *Mar. Ecol. Prog. Ser.* **479**, 47-62. doi:10.3354/meps10193

**Koehl, M. A. R., Perotti, E., Sischo, D., Hata, T. and Hadfield, M. G.** (2022). Effects of currents, waves, and biofilms on motion and surface contacts of tubeworm larvae swimming above or below surfaces. *Mar. Ecol. Prog. Ser.* **686**, 107-126. doi:10.3354/meps14001

**Kroeker, K. J., Kordas, R. L., Crim, R. N. and Singh, G. G.** (2010). Meta–analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology letters,* **13**, 1419-1434. doi:10.1111/j.1461-0248.2010.01518.x

**LaBarbera, M. and Vogel, S.** (1976). An inexpensive thermistor flowmeter for aquatic biology. *Limnol. Oceanog.,* **21**, 750-756. doi:10.4319/lo.1976.21.5.0750

**Lentink, D., Dickson, W. B., Van Leeuwen, J. L. and Dickinson, M. H.** (2009). Leading-edge vortices elevate lift of autorotating plant seeds. *Science* **324**, 1438-1440. doi:10.1126/science.1174196

**Li, C., Wohrl, T., Lam, H. K. and Full, R. J.** (2019). Cockroaches use diverse strategies to self-right on the ground. *J. Exp. Biol.* **222**, jeb186080. doi:10.1242/jeb.186080

**Liao, J. C.** (2007). A review of fish swimming mechanics and behaviour in altered flows. *Phil. Trans. Roy. Soc. B* **362**, 1973-1993. doi:10.1098/rstb.2007.2082

**Lighthill, M. J.** (1971). Large-amplitude elongated-body theory of fish locomotion. *Proc. Roy. Soc. London. Series B. Biol. Sci.* **179**, 125-138.

**Lissaman, P. B. and Shollenberger, C. A.** (1970). Formation flight of birds. *Science* **168**, 1003-1005. doi:10.1126/science.168.3934.1003

**Loudon, C. and Koehl, M. A. R.** (2000). Sniffing by a silkworm moth: Wing fanning enhances air penetration through and pheromone interception by antennae. *J. Exp. Biol.* **203**, 2977-2990. doi:10.1242/jeb.203.19.2977

**Lowell, R. B., Markham, J. H. and Mann, K. H.** (1991). Herbivore-like damage induces increased strength and toughness in a seaweed. *Proc R Soc Lond B,* **243**, 31-38. doi:10.1098/rspb.1991.0006

**MacAyeal, L. C., Riskin, D. K., Swartz, S. M. and Breuer, K. S.** (2011). Climbing flight performance and load carrying in lesser dog-faced fruit bats (*Cynopterus brachyotis*). *J. Exp. Biol.* **214**, 786-793. doi:10.1242/jeb.050195

**Mahjoub, M. S., Souissi, S., Michalec, F. G., Schmitt, F. G. and Hwang, J. S.** (2011). Swimming kinematics of *Eurytemora affinis* (Copepoda, Calanoida) reproductive stages and differential vulnerability to predation of larval *Dicentrarchus labrax* (Teleostei, Perciformes). *J. Plankton Res.* **33**, 1095-1103. doi:10.1093/plankt/fbr013

**Marden, J. H.** (1989). Effects of load–lifting constraints on the mating system of a dance fly. *Ecology* **70**, 496-502. doi:10.2307/1937553

**Martinez, M. M., Full, R. J. and Koehl, M. A. R.** (1998). Underwater punting by an intertidal crab: A novel gait revealed by the kinematics of pedestrian locomotion in air vs. water. *J. Exp. Biol.* **201**, 2609-2623. doi:10.1242/jeb.201.18.2609

**May, R. M., Roughgarden, J. and Levin, S. A.** (eds.) (1989). *Perspectives in Ecological Theory*. Princeton, NJ: Princeton University Press.

**McCay, M. G.** (2001). Aerodynamic stability and maneuverability of the gliding frog *Polypedates dennysi*. *J. Exp. Biol.* **204**, 2817-2826. doi:10.1242/jeb.204.16.2817

**McCay, M. G.** (2003). Winds under the rain forest canopy: The aerodynamic environment of gliding tree frogs. *Biotropica* **3**, 94-102. https://www.jstor.org/stable/30043038

**McGill, B. J., Enquist, B. J., Weiher, E. and Westoby, M.** (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **21**, 178-185. doi:10.1016/j.tree.2006.02.002

**Mead, K. S. and Koehl, M. A. R.** (2000). Stomatopod antennule design: The asymmetry, sampling efficiency, and ontogeny of olfactory flicking. *J. Exp. Biol.* **203**, 3795-3808. doi:10.1242/jeb.203.24.3795

**Monteith, J. and Unsworth, M.** (2013). *Principles of Environmental Physics: Plants, Animals, and the Atmosphere*, 4th edn. San Diego: Academic Press.

**Mountcastle, A. M. and Combes, S. A.** (2013). Wing flexibility enhances load-lifting capacity in bumblebees. *Proc Roy. Soc. B* **280**, 20130531. doi:10.1098/rspb.2013.0531

**Muijres, F. T., Chang, S. W., van Veen, W. G., Spitzen, J., Biemans, B. T., Koehl, M. A. R. and Dudley, R.** (2017). Escaping blood-fed malaria mosquitoes minimize tactile detection without compromising on take-off speed. *J. Exp. Biol.* **220**, 3751-3762. doi:10.1242/jeb.163402

**Müller, U. K.** (2003)). Doctor Pangloss retires from biomechanics: Vertebrate biomechanics and evolution. *J. Exp. Biol.* **206**, 1602-1603. doi:10.1242/jeb.00304

**Murdock, G. R. and Currey, J. D.** (1978). Strength and design of shells of the two ecologically distinct barnacles, *Balanus balanus* and *Semibalanus* (*Balanus*) *balanoides* (Cirripedia). *Biol. Bull.* **155**, 169-192. doi:10.2307/1540874

**Niklas, K. J.** (1982). Simulated and empiric wind pollination patterns of conifer ovulate cones. *Proc. Nat. Acad. Sci.* **79**, 510-514. doi:10.1073/pnas.79.2.510

**Niklas, K. J.** (1985). The aerodynamics of wind pollination. *Bot. Rev.* **51**, 328-386. doi:10.1007/BF02861079

**Niklas, K. J.** (1992). *Plant Biomechanics: An Engineering Approach to Plant Form and Function*. Chicago: University of Chicago Press.

**Norberg, U. M.** (1990). *Vertebrate Flight*. Berlin: Springer.

**Norton, T. A., Mathieson, A. C. and Neushul, M.** (1982). A review of some aspects of form and function in seaweeds. *Bot. Marina* **25**, 510. doi:10.1515/botm.1982.25.11.501

**Nudds, R. L. and Bryant, D. M.** (2002). Consequences of load carrying by birds during short flights are found to be behavioral and not energetic. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **283**, R249-R256. doi:10.1152/ajpregu.00409.2001

**O'Donnell, M. J. and Denny, M. W.** (2008). Hydrodynamic forces and surface topography: Centimeter–scale spatial variation in wave forces. *Limnol. Oceanog.* **53**, 579-588. doi:10.4319/lo.2008.53.2.0579

**O'Donnell, M. J., George, M. N. and Carrington, E.** (2013). Mussel byssus attachment weakened by ocean acidification. *Nature Climate Change* **3**, 587-590. doi:10.1038/nclimate1846

**Okamura, B.** (1984). The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of Bryozoa. I. *Bugula stolonifera* (Ryland), an arborescent species. *J. Exp. Mar. Biol. Ecol.* **83**, 179-193. doi:10.1016/0022-0981(84)90044-3

**Okamura, B.** (1986). Group living and the effects of spatial position in aggregations of *Mytilus edulis*. *Oecologia* **69**, 341-347. doi:10.1007/BF00377054

**Ortega-Jimenez, V. M., Sapir, N., Wolf, M., Variano, E. A. and Dudley, R.** (2014). Into turbulent air: Size-dependent effects of von Karman vortex streets on hummingbird flight kinematics and energetics. *Proc. R. Soc. B* **281**, 20140180. doi:10.1098/rspb.2014.0180

**Padilla, D. K.** (1985). Structural resistance of algae to herbivores. *Mar. Biol.,* **90**, 103-109. doi:10.1007/BF00428220

**Pan, Y. and Dong, H.** (2020). Computational analysis of hydrodynamic interactions in a high-density fish school. *Phys. Fluids* **32**, 121901. doi:10.1063/5.0028682

**Patek, S. N. and Longo, S. J.** (2018). Evolutionary biomechanics: The pathway to power in snapping shrimp. *Current Biol.* **28**, R115-R117. doi:10.1016/j.cub.2017.12.033

**Patterson, M. R., Harwell, M. C., Orth, L. and Orth, R.** (2001). Biomechanical properties of the reproductive shoots of eelgrass. *Aquat. Bot.* **69**, 27-40. doi:10.1016/S0304-3770(00)00133-9

**Pentcheff, N. D.** (1991). Resistance to crushing from wave-borne debris in the barnacle, *Balanus glandula*. *Mar. Biol.* **110**, 399-408. doi:10.1007/BF01344359

**Pennycuick, C. J.** (1968). A wind-tunnel study of gliding flight in the pigeon *Columba livia*. *J. Exp. Biol.* **49**, 509-526. doi:10.1242/jeb.49.3.509

**Pepper, R., Jaffe, J. S., Variano, E. and Koehl, M. A. R.** (2015). Zooplankton in flowing water near benthic communities encounter rapidly fluctuating velocity gradients and accelerations. *Mar. Biol.* **162**, 1939-1954. doi:10.1007/s00227-015-2713-x

**Platt, T. and Denman, K. L.** (1975). Spectral analysis in ecology. *Ann. Rev. Ecol. Syst.* **6**, 189-210. doi:10.1146/annurev.es.06.110175.001201

**Porter, W. P., Mitchell, J. W., Beckman, W. A. and Tracy, C. R.** (1975). Environmental constraints on some predator-prey interactions. In *Perspectives of Biophysical Ecology* (ed. D. M. Gates and R. B. Schmerl), pp. 347-364. New York: Springer-Verlag.

**Rayner, J.** (1981). Flight adaptations in vertebrates. *Symp. Zool. Soc. London* **48**, 137-172.

**Reidenbach, M. A., Koseff, J. R., Monismith, S. G., Steinbuck, J. V. and Genin, A.** (2006). The effects of waves and morphology on mass transfer within branched reef corals. *Limnol. Oceanogr.* **51**, 1134-1141. doi:10.4319/lo.2006.51.2.1134

**Reidenbach, M. A., George, N. and Koehl, M. A. R.** (2008). Antennule morphology and flicking kinematics facilitate odor sampling by the spiny lobster, *Panulirus argus*. *J. Exp. Biol.* **211**, 2849-2858. doi:10.1242/jeb.016394

**Reidenbach, M. A., Koseff, J. R. and Koehl, M. A. R.** (2009). Hydrodynamic forces on larvae affect their settlement on coral reefs in turbulent, wave-driven flow. *Limnol. Oceanogr.* **54**, 318-330. doi:10.4319/lo.2009.54.1.0318

**Rubenstein, D. I. and Koehl, M. A. R.** (1977). The mechanisms of filter feeding: Some theoretical considerations. *Amer. Natur.* **111**, 981-994. doi:10.1086/283227

**Saadat, M., Berlinger, F., Sheshmani, A., Nagpal, R., Lauder, G. V. and Haj-Hariri, H.** (2021). Hydrodynamic advantages of in-line schooling. *Bioinsp. Biomim.* **16**, 046002. doi:10.1088/1748-3190/abe137

**Schoener, T. W.** (1986). Mechanistic approaches to community ecology: A new reductionism? *Am. Zool.* **26**, 81-106. doi:10.1093/icb/26.1.81

**Shimeta, J. and Jumars, P. A.** (1991). Physical mechanisms and rates of particle capture by suspension feeders. *Oceanogr. Mar. Biol. Annu. Rev.* **29**, 191-257.

**Sirison, N. and Burnett, N. P.** (2020). *Turbinaria ornata* (Phaeophyceae) varies size and strength to maintain environmental safety factor across flow regimes. *J. Phycol.* **56**, 233-237. doi:10.1111/jpy.12933

**Sponberg, S. and Full, R. J.** (2008). Neuromechanical response of musculoskeletal structures in cockroaches during running on rough terrain. *J. Exp. Biol.* **211**, 433-446. doi:10.1242/jeb.012385

**Stewart, H. L.** (2006). Ontogenetic changes in tissue strength, buoyancy and reproductive investment in the tropical rafting macroalga *Turbinaria ornata*. *J. Phycol.* **42**, 43-50. doi:10.1111/j.1529-8817.2006.00184.x

**Sutherland, K. R., Dabiri, J. O. and Koehl, M. A. R.** (2011). Simultaneous field measurements of ostracod swimming behavior and background flow. *Limnol. Oceanog. Fluids Environ.* **1**, 135-146. doi:10.1215/21573698-1472410

**Svetlichny, L., Hubareva, E. and Isinibilir, M.** (2017). Comparative trends in respiration rates, sinking and swimming speeds of copepods *Pseudocalanus elongatus* and *Acartia clausi* with comments on the cost of brooding strategy. *J. Exp. Mar. Biol. Ecol.* **488**, 24-31. doi:10.1016/j.jembe.2016.12.005

**Tickle, P. G., Lean, S. C., Rose, K. A. R., Wadugodapitiya, A. P. and Codd, J. R.** (2013). The influence of load carrying on the energetics and kinematics of terrestrial locomotion in a diving bird. *Biol. Open* **2**, 1239-1244. doi:10.1242/bio.20135538

**Tunnicliffe, V.** (1981). Breakage and propagation of the stony coral *Acropora cervicornis*. *Proc. Nat. Acad. Sci. USA* **78**, 2427-2431. doi:10.1073/pnas.78.4.2427

**Usherwood, J. R., Stavrou, M., Lowe, J. C., Roskilly, K. and Wilson, A. M.** (2011). Flying in a flock comes at a cost in pigeons. *Nature* **474**, 494-497. doi:10.1038/nature10164

**Vincent, J. F.** (1975). Locust oviposition: Stress softening of the extensible intersegmental membranes. *Proc. Roy. Soc. Lond. B* **188**, 189-201. doi:10.1098/rspb.1975.0012

**Vincent, J.** (2012). *Structural Biomaterials*, 3rd edn. Princeton: Princeton University Press.

**Vogel, S.** (1994). *Life in Moving Fluids: The Physical Biology of Flow*, 2nd edn. Princeton: Princeton University Press.

**Vogel, S.** (1984). Drag and flexibility in sessile organisms. *Am. Zool.* **24**, 37-44. doi:10.1093/icb/24.1.37

**Vogel, S.** (2013). *Comparative Biomechanics: Life's Physical World, Second Edition*. Princeton: Princeton University Press.

**Vogel, S. and Wainwright, S. A.** (1969). *A Functional Bestiary: Laboratory Studies About Living Systems*. Reading, MA: Addison-Wesley Publishing Company.

**Wainwright, P. C.** (2007). Functional versus morphological diversity in macroevolution. *Ann. Rev. Ecol. Evol. Syst.* **38**, 381-401. doi:10.1146/annurev.ecolsys.38.091206.095706

**Wainwright, P. C. and Reilly, S. M.** (1994). *Ecological Morphology: Integrative Organismal Biology.* Chicago: University of Chicago Press.

**Wainwright, S. A. and Koehl, M. A. R.** (1976). The nature of flow and the reaction of benthic cnidaria to it. In *Coelenterate Ecology and Behavior* (ed. G. O. Mackie), pp. 5-21. Boston, MA: Springer.

**Wainwright, S. A., Biggs, W. D., Currey, J. D. and Gosline, J. M.** (1976). *Mechanical Design in Organisms*. London: Edward Arnold.

**Waldrop, L. D. and Koehl, M. A. R.** (2016). Do terrestrial hermit crabs sniff? Air flow and odorant capture by flicking antennules. *J. Roy. Soc. Interface* **13**, 20150850. doi:10.1098/rsif.2015.0850

**Waldrop, L. D., Hann, M., Henry, A., Kim, A., Punjabi, A. and Koehl, M. A. R.** (2015). .Ontogenetic changes in the olfactory antennules of the shore crab, *Hemigrapsus oregonensis*, maintain sniffing function during growth. *J. R. Soc. Interface* **12**, 20141077. doi:10.1098/rsif.2014.1077

**Wang, C., Li, Q. Y., Wang, S. N., Qu, S. X. and Wang, X. X.** (2014). Microstructure and self-sharpening of the magnetite cap in chiton tooth. *Mat. Sci. Engin. C.* **37**, 1-8. doi:10.1016/j.msec.2013.12.029

**Webb, P. W.** (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Board Can.* **190**, 1-158.

**Webb, P. W.** (1984). Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* **24**, 107-120. doi:10.1093/icb/24.1.107

**Webb, P. W. and Weihs, D.** (ed.) (1983). *Fish Biomechanics*. Westport, CT: Praeger.

**Weibel, D. B., Garstecki, P., Ryan, D., DiLuzio, W. R., Mayer, M., Seto, J. E. and Whitesides, G. M.** (2005). Microoxen: Microorganisms to move microscale loads. *Proc. Nat. Acad. Sci.* **102**, 11963-11967. doi:10.1073/pnas.0505481102

**Weihs, D.** (1974). Energetic advantages of burst swimming of fish. *J. Theor. Biol.* **48**, 215-229. doi:10.1016/0022-5193(74)90192-1

**Weihs, D.** (1975). Some hydrodynamical aspects of fish schooling. In *Swimming and Flying in Nature* (ed. T. Y. T. Wu, C. J. Brokaw and C. Brennen), pp. 703-718. Boston, MA: Springer.

**West-Eberhard, M. J.** (2003). *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.

**Wolcott, B. D.** (2007). Mechanical size limitation and life-history strategy of an intertidal seaweed. *Mar. Ecol. Prog. Ser.* **338**, 1-10. doi:10.3354/meps338001

**Yasa, O., Erkoc, P., Alapan, Y. and Sitti, M.** (2018). Microalga–powered microswimmers toward active cargo delivery. *Adv. Materials* **30**, 1804130. doi:10.1002/adma.201804130

**Zhou, Z., Barrett, P. M. and Hilton, J.** (2003). An exceptionally preserved lower Cretaceous ecosystem. *Nature* **421**, 807-814. doi:10.1038/nature01420