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A Life Outside

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Abstract

How do the morphologies of organisms affect their physical interactions with the environment and other organisms? My research in marine systems couples field studies of the physical habitats, life history strategies, and ecological interactions of organisms with laboratory analyses of their biomechanics. Here, I review how we pursued answers to three questions about marine organisms: (*a*) how benthic organisms withstand and utilize the water moving around them, (*b*) how the interaction between swimming and turbulent ambient water flow affects where small organisms go, and (*c*) how hairy appendages catch food and odors. I also discuss the importance of different types of mentors, the roadblocks for women in science when I started my career, the challenges and delights of interdisciplinary research, and my quest to understand how I see the world as a dyslexic.

> Those who have never entered upon scientific pursuits know not a tithe of the poetry by which they are surrounded.
>
> —Herbert Spencer (1859, p. 19)

1. INTRODUCTION

I study the physics of how organisms interact with each other and their environments. I am fascinated by biological form, so the goal of my research is to elucidate basic physical rules that explain how morphology affects the mechanical functions of organisms. Such physical rules apply across taxa and can help us understand the performance of diverse types of creatures in different habitats. I combine techniques from fluid and solid mechanics with those from biology and ecology to do experiments in the field as well as in the laboratory. The various questions my students and I have been studying are summarized on our lab website (**https://ib.berkeley.edu/labs/koehl**). Here, I highlight three examples of scientific questions that intrigued me over the years, focusing on the process of discovery rather than providing an exhaustive literature review. I devote the second part of this memoir to touch on some bits of my history that taught me important lessons, which I would like to share with young scientists. A biography of me written for middle schoolers (Parks 2005, part of a book series by the National Academy of Sciences to interest children in STEM) describes my personal and professional history, so I'll skip those details here.

1.1. Comparative Biomechanics

Newton's laws apply to living things. We can use physics to learn about how the morphology of organisms, from tissue microarchitecture to whole-body size and shape, affects their performance of mechanical functions such as feeding, locomotion, or resistance to breakage. Although most biomechanical research focuses on humans, comparative biomechanics studies the biofluiddynamics (sensu Lighthill 1975) and structural design of diverse types of organisms (e.g., Wainwright et al. 1976; Niklas 1992; Vogel 1994, 2013). Quantitative relationships between measured structural variables and defined aspects of biomechanical function are usually not linear. Thus, these biomechanical relationships allow us to identify whether differences in morphology have minor effects on performance or have serious consequences. They also predict how size changes (during ontogeny or evolution) can lead to novel biomechanical functions (reviewed in Koehl 1996b, 2000, 2023; Kempes et al. 2019).

1.2. Interface Between Biomechanics and Ecology

The biological structures we study evolved in the complex, variable natural world, where organisms interact with turbulent ambient water flow or wind, intricate terrain, and other organisms. Therefore, if we seek to understand the functional consequences of various aspects of an organism's morphology, we must measure the physical and biological environment as it is encountered by that organism throughout its ontogeny. By coupling field studies of the physical habitats, life history strategies, and ecological interactions of organisms with laboratory or field analyses of their biomechanics, we can determine which physical functions are important to their growth, survival, and fitness (reviewed in Koehl 2023).

Interdisciplinary research combining biomechanics and ecology has revealed how biomechanical mechanisms affect ecological processes (ecological biomechanics, reviewed in Koehl 1989, 1996b, 1999; Denny & Gaylord 2010; Denny 2016) and, conversely, how the ecology of organisms determines their biomechanical performance (mechanical ecology, reviewed in Bauer et al.

2020; Koehl 2022, 2023). By working at the interface between biomechanics and ecology, I have investigated a number of questions about marine organisms, three of which I review here.

2. QUESTIONS

2.1. How Do Benthic Organisms Withstand and Utilize the Water Moving Around Them?

Benthic marine organisms, especially those attached to the substratum (sessile organisms), risk being dislodged or broken by ocean currents and waves, yet they also depend on the water moving around them for transport of critical materials. Ambient water flow carries dissolved substances (gases, nutrients, and chemical signals) and particulate food to benthic organisms, removes their wastes, transports and mixes their gametes, and disperses their larvae or spores. Therefore, the functional designs of benthic organisms should represent trade-offs between maximizing (for transport) and minimizing (for avoiding damage) the effects of ambient water flow.

I first became interested in the hydrodynamics of benthic organisms as a graduate student when I was investigating how soft-bodied hydrostatic organisms withstand large mechanical loads. I thought sea anemones that lived on wave-battered rocky shores would be a good research system (**Figure 1**). To design biomechanical laboratory tests, I needed to calculate the hydrodynamic drag pushing the anemones downstream, so I had to know the water velocity. Rather than grabbing values from oceanography books for water velocities in waves, I went outside where the anemones lived and set up flow probes in their habitats (**Figure 2*a***). I measured not only freestream velocities in waves rushing through the channels but also velocities along the floors of the channels where the anemones lived.

2.1.1. Flow microhabitats. When I set off to make these measurements, marine biologists classified field sites in terms of their exposure to waves, so we assumed that all the organisms on exposed shores encountered faster water flow than did organisms living at sites protected from big waves and rapid currents. To my surprise, in exposed surge channels swept by waves with peak velocities of ~6 m s^{-1} (**Figure 1*a***), I discovered that the sea anemones flattened themselves on the floor of the channel (**Figure 1*b***) and encountered peak velocities of only ~0.1 m s^{-1} (Koehl 1977a, 1982). They were hardly exposed, although the taller kelp growing next to them were hit by rapid

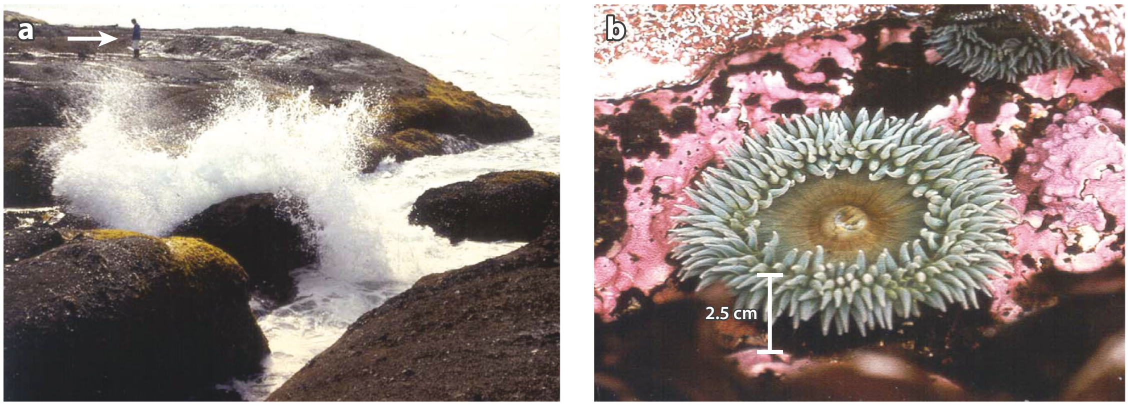


Figure 1

A surge channel on Tatoosh Island, Washington. (*a*) A wave flowing into the channel during a rising tide (this channel is shown at low tide in **Figure 2*a***). The arrow indicates a person for scale. (*b*) Green sea anemones, *Anthopleura xanthogrammica*, living on the floor of the surge channel.

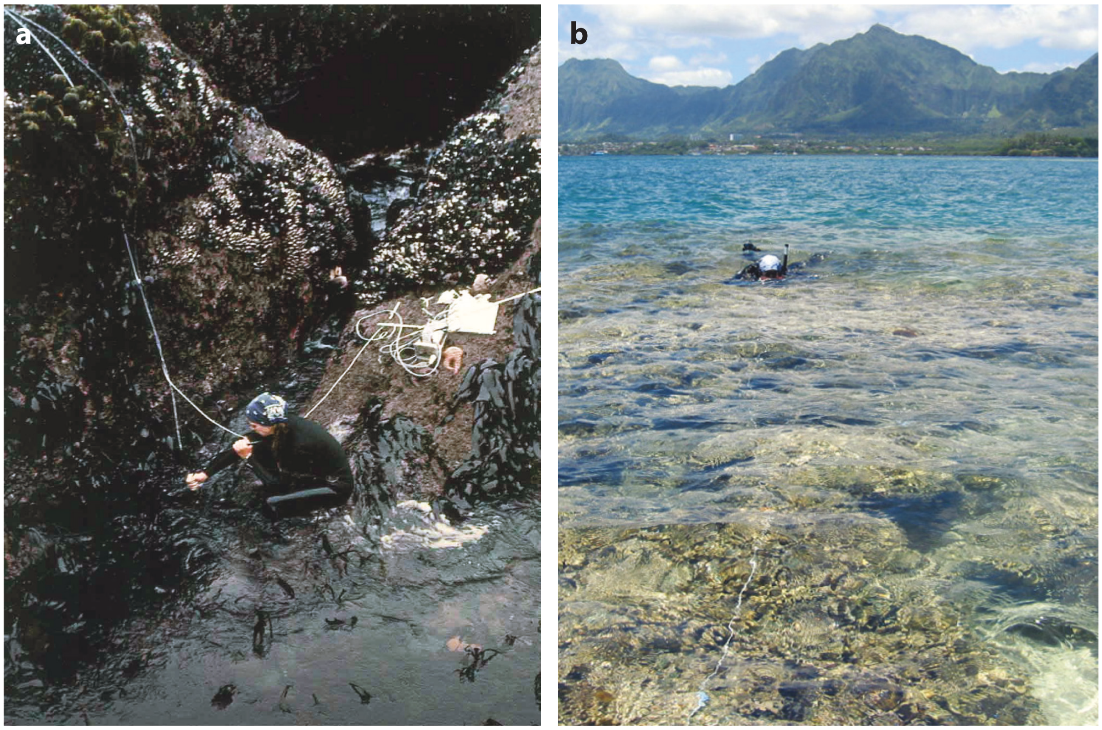
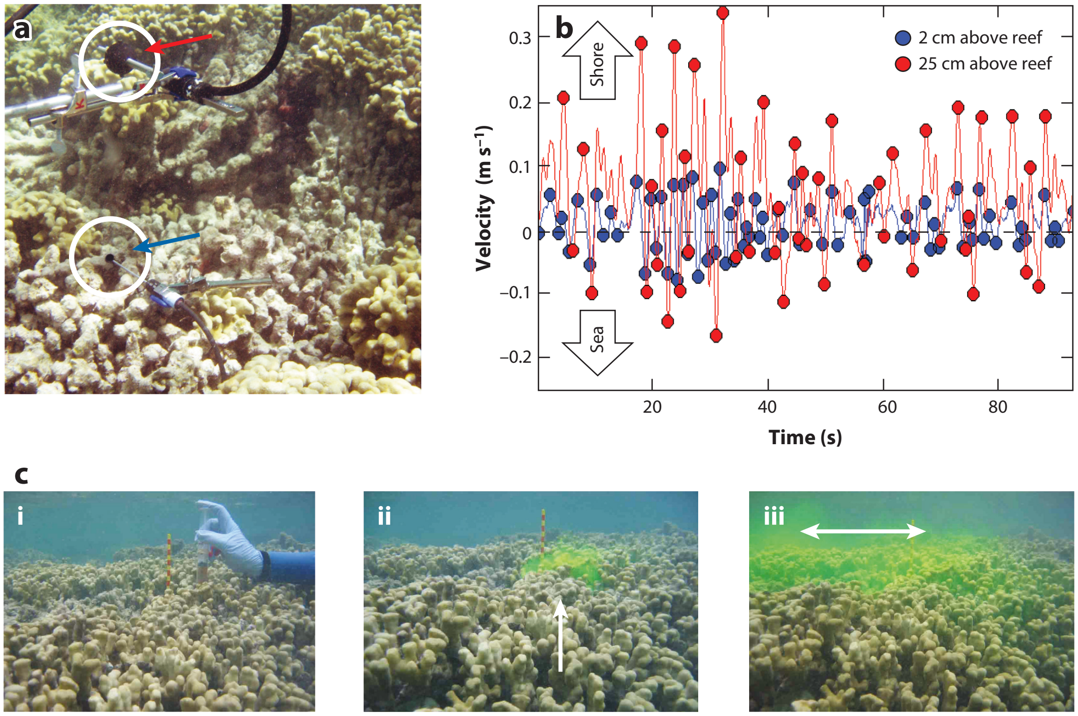


Figure 2

The author in the field. Taking field measurements of the physical environment on the scales encountered by the organisms is essential to understanding their biomechanical function in nature. (*a*) The author setting up an electromagnetic flow probe at low tide in a surge channel on Tatoosh Island, Washington, in 1974 to record wave-driven flow throughout the tidal cycle encountered by sea anemones. Photo by C. Birkeland. (*b*) The author running a transect across a coral reef in Kaneohe Bay, Hawaii, to measure effects of algal overgrowth on water flow into and out of the reef as part of a current study of the physics of larval settlement onto benthic communities exposed to turbulent, wave-driven water flow. Photo by M. Hadfield.

flow (Koehl 1999, 2022). I was also amazed that anemones at protected sites with peak freestream velocities of only $\sim$0.5 m s^{-1} stood taller and encountered the same maximum velocities as their conspecifics in exposed surge channels. These data made me realize that organisms live in microhabitats that can be very different from the conditions that we researchers experience at a site. I learned the importance of measuring the environment on the spatial scale of the organisms being studied, and I learned about benthic boundary layers.

When water flows along a surface, the layer in contact with the surface does not slip relative to the surface, so a velocity gradient (boundary layer) develops in the water between the surface and the freestream flow. Because flow close to the substratum is slowed (e.g., Koehl 1982, Jumars & Nowell 1984) (**Figure 3*a*,*b***), tall organisms in benthic communities encounter faster water motion than do their shorter neighbors. Local topography alters the ambient flow experienced by an individual, and organisms in the middle of aggregations (e.g., seagrass meadows and kelp beds) experience slower flow than those along the edges (Koehl 2022, 2023). For example, we found that water velocities 2 cm above coral reefs exposed to waves with peak velocities of $>$1 m s^{-1} were only $\sim$0.3 m s^{-1}, while velocities in the spaces between coral branches within the reef were $\sim$0.08 m s^{-1} (Koehl & Hadfield 2004). In laboratory flumes, we can mimic the waves, boundary layer, and turbulence spectrum measured in the field and use particle image velocimetry (PIV) and



Dye is injected into the reef

Odor-bearing water moves up out of the reef

Odor spreads along the reef surface

Figure 3

Water flow above a coral reef in Kaneohe Bay, Hawaii (this reef is also shown in **Figure 2*b***). (*a*) An electromagnetic flow probe 25 cm above the reef surface (*red arrow*) and a miniaturized electromagnetic flow probe 2 cm above the reef surface (*blue arrow*). (*b*) The horizontal component of the water velocity measured at heights of 25 cm (*red*) and 2 cm (*blue*) above the reef by the probes shown in panel *a*. Water motion in waves is orbital, so the horizontal velocity components of this wave-driven flow move shoreward (positive velocities) and seaward (negative velocities). Dots show peak shoreward and seaward velocities attained in successive waves. The flow is much slower close to the reef surface. (*c*) Using dye to investigate how odor-bearing reef water moves up into the wavy water above a reef. (*i*) Fluorescein dye is injected into the interstices between the branches of coral, *Porites compressa*, to label the odor-bearing water from within the reef. (*ii*) In the orbital water motion of waves, water moves vertically into and out of the reef, but with a net flow upward at convex and flat regions of the reef (dye moving up out of the reef is pictured here) and a net flow downward in depressions between coral heads. (*iii*) Shear is high between the slowly moving water within a reef and the water flowing more rapidly right above the reef, so odor-bearing water flowing out of the reef spreads along the surface of the reef.

laser Doppler velocimetry (LDV) to measure instantaneous velocities near benthic communities on even finer scales (Koehl & Reidenbach 2008, Reidenbach et al. 2009, Koehl et al. 2013, Pepper et al. 2015). PIV reveals the instantaneous local water acceleration above and slow eddies behind organisms on the substratum (**Figure 4*a*,*b***). LDV measurements showed that newly settled larvae only 200 μm tall sitting on top of a coral reef in flow like that in **Figure 3*b*** experience peak velocities of ∼0.1 m s^{-1}, while larvae on surfaces within the reef see peaks of only ∼0.02 m s^{-1} (Reidenbach et al. 2009, Koehl 2023). LDV can resolve flow microhabitats produced by tiny topographic features (<1 mm), as we found in fouling communities (Koehl et al. 2013).

2.1.2. Morphology affects hydrodynamic forces on organisms and stresses in their tissues.

The size, shape, and flexibility of organisms determine the magnitudes of the hydrodynamic forces they experience when exposed to the water motion in their microhabitats. By studying different

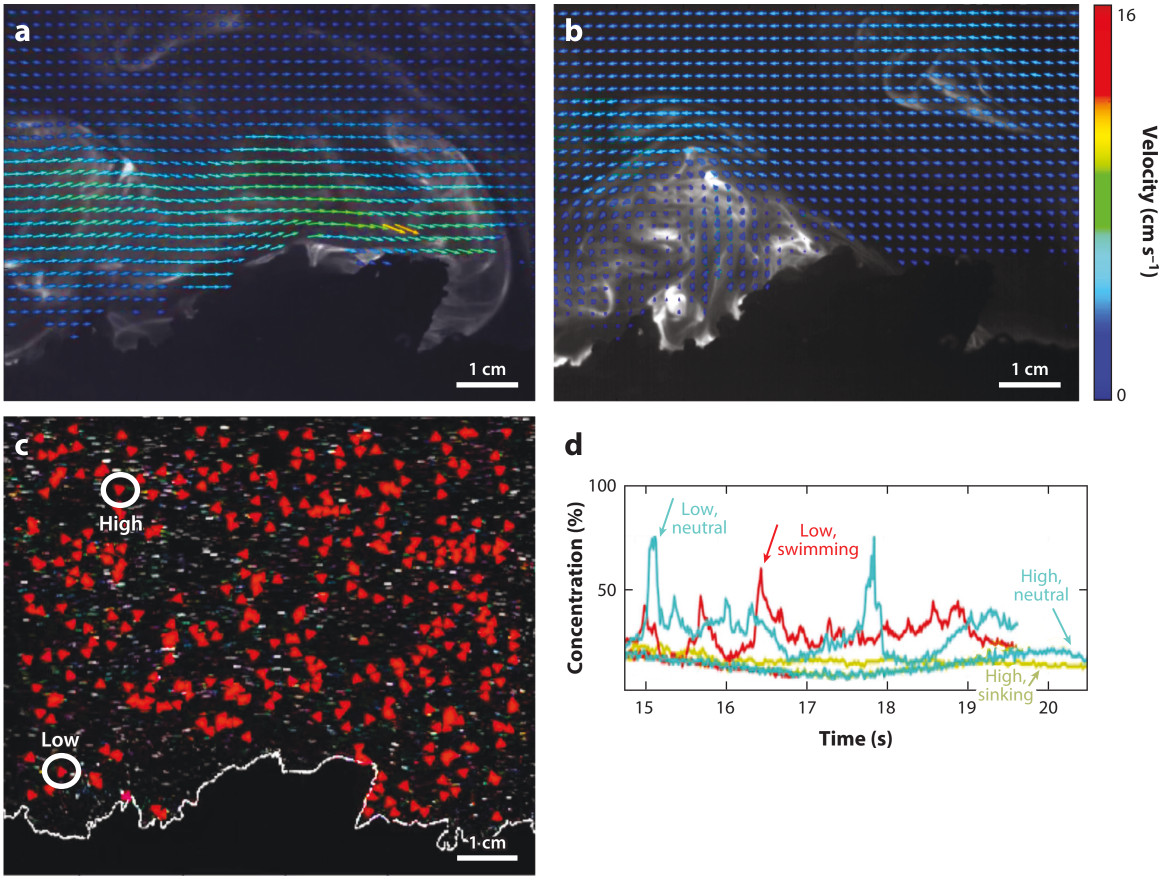


Figure 4

Agent-based models of larvae in simultaneous particle image velocimetry (PIV) and planar laser-induced fluorescence (PLIF) data measured over a fouling community in a wave flume. (*a*) Example of instantaneous velocity vectors (color scale to the right of panel *b*) and concentrations of dye (to simulate odors; lighter pixels indicate higher concentrations) released from the benthos. At this instant, water was flowing to the right. (*b*) Instantaneous PIV/PLIF data measured as the flow was reversing to begin moving to the left. (*c*) Randomly chosen positions of agents (model larvae) in the water above the fouling community at the start of the PIV/PLIF data. (*d*) Dye concentrations encountered by different model larvae. The larvae were assigned different behaviors: Red denotes that the larva swam forward continuously at 2 mm s^{-1}, so its direction of motion changed as it was rotated by local instantaneous vorticity; blue denotes that the larva was passive and neutrally buoyant; and chartreuse denotes that the larva was passive and sank at 2 mm s^{-1}. Larvae with these behaviors that had the starting positions labeled as high and low in panel *c* were followed with time, and examples of the concentrations of dye (as a percentage of the concentration at the benthos surface) encountered by each as a function of time are plotted here. The frequency of encounters with filaments of high concentration is much higher when larvae are close to the surface.

types of sessile marine animals and seaweeds, we found that hydrodynamic forces are lowered by features that reduce the size of the messy wake that forms downstream of an organism, while features that increase wake size enhance exchange of materials between the organism and the surrounding water (Koehl 1977a, 1984a, 1986, 1999, 2022; Koehl & Alberte 1988; Koehl et al. 2008).

Not only can organism morphology and behavior affect the magnitude of the hydrodynamic forces they experience, but their structure also determines how big the stresses are in their tissues when subjected to such loads (stress is force per cross-sectional area of material resisting a load). We calculate stress distributions in organisms using the same physical rules that structural engineers employ to analyze beams and buildings (Wainwright et al. 1976). We have found that, for parts of organisms that are bent or twisted by flowing water, stresses are lower in short, wide structures than in long, slender ones, and if structures are pulled, the stresses are lower still (Koehl 1977c, 1982, 1984a). We learned that organisms of different shapes exposed to the same water flow can experience different stresses, and that organisms in protected habitats sometimes experience larger stresses than do those at exposed sites.

By studying organism tissues using mechanical tests developed by materials scientists (e.g., Wainwright et al. 1976, Koehl & Wainwright 1984, Vincent 2012), we measured their stiffness, resilience, strength, and toughness (Koehl 1977b, 1982, 1999; Koehl & Wainwright 1977; Holbrook et al. 1991; Johnson & Koehl 1994; Burnett & Koehl 2019, 2021; Koehl & Daniel 2022). With that information, we could predict how much they deform and whether they break under different environmental conditions. Some organisms change their patterns of growth in response to the magnitude of stress in their tissues, thereby assuming shapes that enhance their performance in different flow habitats (e.g., Koehl et al. 2008, Koehl & Silk 2021). We have also discovered that some organisms have surprisingly bad engineering designs (Koehl 2023). That led me to step back and consider the range of timescales that are important to the survival, reproduction, and fitness of different types of organisms exposed to ambient water flow.

2.1.3. Temporal variation.

My field measurements showed me that flow on benthic organisms varied with time. Velocities fluctuated over fractions of a second in turbulence, seconds as waves rushed back and forth (**Figures 3*a*** and **4*a*,*b***), hours as the tide ebbed and flowed, days as the weather changed, and months to years as seasonal storms came and went.

When I was a graduate student, most studies of organism fluid mechanics were steady-state analyses (velocity is constant). Since I measured high water acceleration in waves, I had to learn about non-steady-state hydrodynamics and how to determine instantaneous acceleration reaction forces on anemones to add to the drag they experienced (Koehl 1977a). It was an exciting time, when non-steady-state analyses of swimming and flying were blossoming while we were trying to understand organisms battered by waves (Koehl 1984a, Denny et al. 1985, Denny 1988). Because water in waves flows back and forth, flexible macrophytes move with the flow and experience low mechanical stress until they are jerked to a halt at the end of their tethers, so wave period determines whether long seaweeds experience higher or lower stresses than short ones (Koehl 1984a, 1986, 1999, 2022; Gaylord & Denny 1997; Denny et al. 1998; Wolcott 2007).

Most tissues and skeletal materials have time-dependent mechanical properties, so their deformability and resistance to breakage depend on the rates, durations, and frequencies of forces they experience (Wainwright et al. 1976, Vincent 2012). For example, when the viscoelastic connective tissue of the body walls of sea anemones was subjected to stress regimes mimicking those experienced in nature, I discovered that it is stiff and resilient when subjected to brief stresses simulating repetitive stretching by waves, but can be extended to twice its resting length when subjected overnight to low stress due to the small internal pressure sea anemones use to inflate themselves (Koehl 1977b). Frond tissue of some macroalgae is stronger when stretched rapidly to simulate wave impingement than when pulled more slowly (Burnett & Koehl 2021). The shear-thinning mucus attaching a sea-slug larva to a surface acts like an elastic bungee cord when hit with pulses of flow like those that larvae encounter on coral reefs, but it flows like a liquid and breaks at low stress if subjected to the steady shear flow traditionally used to measure adhesive strengths of microorganisms (Koehl 2023).

Engineers use the safety factor (the ratio of breaking stress to maximum stress encountered during a structure's lifetime) to describe the likelihood that a structure will fail. 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, we proposed an ecologically relevant measure of likelihood of failure: 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 organism's habitat during that life stage (Johnson & Koehl 1994). ESF can change during the life of an organism, and low ESF correlates with the times during ontogeny and the seasons when organisms are broken (Johnson & Koehl 1994, Stewart 2006, Wolcott 2007, Koehl & Daniel 2022). Organisms face trade-offs between investment in mechanical support and investment in reproduction, and different life history strategies balance these two factors (Koehl 2023). Some macroalgae grow quickly and reproduce before winter storms wash them away (low ESF in winter) (Johnson & Koehl 1994, Koehl 1999, Koehl & Daniel 2022). Others grow slowly, build strong thalli that survive storms (high ESF year-round), and reproduce year after year (Koehl 1999). Life history explains why so many organisms with bad engineering designs are successful in high-flow habitats.

2.2. How Does the Interaction Between Swimming and Ambient Water Flow Affect Where Small Organisms Go?

When microorganisms swim in the ocean, they are also carried by turbulent ambient currents that often move faster than the tiny creatures can locomote. Studies and models of swimming and chemotaxis by microorganisms are usually conducted in still water, whereas large-scale models of microorganism transport by ambient flow treat them as passive tracers. How does the interaction between a microorganism's swimming through the water and its transport and rotation by turbulent ambient flow affect where it travels through the habitat, and what are the environmental signals it encounters along the way?

Many bottom-dwelling marine animals produce microscopic larvae that are dispersed to new sites by ambient water currents and then must land on surfaces in suitable habitats. These larvae provide a good system for studying how microscopic swimmers navigate in ambient flow because they are weak swimmers with somewhere specific to go: They need to travel through moving water to land on the right kind of benthic community. I am investigating how they do this with larval biologist Mike Hadfield, focusing on coral reefs (**Figures 2*b*** and **3**) and fouling communities (**Figure 4**).

Although some larvae respond to dissolved chemical cues (odors) in a dish, there was a debate about whether such slow swimmers could use odors from the benthos to navigate to appropriate settlement sites in turbulent flow in the field. How are the concentrations of odors from the benthos dispersed in turbulent flow, and can the responses of weakly swimming larvae to these odors affect their chances of landing on a suitable habitat? We first studied this question using larvae of the sea slug *Phestilla sibogae*, which are induced to undergo metamorphosis by a dissolved chemical cue released into the water by the coral *Porites compressa* (Hadfield & Paul 2001). We found that water samples from the interstices in Hawaiian coral reefs contained this coral odor cue (Koehl & Hadfield 2004). Dye studies revealed that this odor-bearing reef water moved up into the wavy water above a reef, where it spread along the reef (**Figure 3*c***). Odor plumes like this have been analyzed as diffusing clouds, but what are the concentrations of coral cue encountered by a microscopic larva swimming in the waves above a reef? Over a coral reef in a wave flume exposed to flow mimicking that in the field, we used a sheet of laser light to illuminate a millimeter-thick slice of water where we could see the dye-labeled water coming from the reef [planar laser-induced fluorescence (PLIF)] and made videos of the instantaneous fine-scale distribution of odor concentrations in the water (Koehl et al. 2007, Reidenbach et al. 2007). We discovered that on the scale of a microscopic larva, there were fine filaments of odor swirling around in odor-free water. PLIF also revealed such swirling odor filaments in the water next to fouling communities exposed to wavy flow (**Figures 4*a*,*b***).

What is the time course of odor concentrations encountered by a larva carried in wavy, turbulent flow? We used agent-based modeling, which follows autonomous decision-making agents that individually assess their situation and take actions based on a set of rules (e.g., Bonabeau 2002), to put computer larvae into random positions in our PIV/PLIF data (**Figure 4*c***). At each time step, a larva swam through the water at the speed of real larvae, and was also carried by the moving parcel of water around it and rotated to a new swimming direction by the local vorticity (spinning) of the turbulent water. By riding along the trajectory of a larva, we could plot the cue concentrations (**Figure 4*d***) and hydrodynamic signals (acceleration and shear) it experienced, and we found that the frequency of encounters with short pulses of odor or hydrodynamic signals increased as the larva approached the substratum (Koehl & Cooper 2015, Pepper et al. 2015, Koehl 2023). We have been using fluidic devices to expose larvae to realistic patterns of encounters with odors or hydrodynamic signals, and microvideography to record their responses (Hadfield & Koehl 2004, Koehl 2023). Larvae of *P. sibogae* stopped swimming and sank when entering a filament of coral cue above threshold concentration and resumed swimming upon exiting the filament. By putting larvae with this behavior in our PLIF data for coral reefs, we found that this simple on–off response to the cue enhanced their settlement rates onto the reef by ∼20% (Koehl et al. 2007). When we tested the model in the field, the spatial pattern of recruitment of *P. sibogae* to reefs matched model predictions (Hadfield et al. 2006).

Sinking when exposed to chemical or hydrodynamic signals that indicate that a surface is nearby (e.g., more frequent encounters with pulses of flow or odors from the surface; **Figure 4*d***) would be a bad strategy for larvae of fouling community animals that land on ship bottoms above them and pilings next to them. By modeling larvae with different behaviors, we found that if a larva cannot predict the direction of a surface, the best strategy for enhancing contact with the surface is to swim continuously (Koehl & Cooper 2015). Thus, by studying navigation on the scale of larvae in turbulent flow, we are discovering that the behavior of tiny, weak swimmers can bias the way that the ambient water flow transports them. Similar fine-scale modeling reveals how zooplankton can surf on turbulence to enhance their vertical motion (Monthiller et al. 2022).

2.3. How Do Hairy Appendages Catch Food and Odors?

Many different types of animals use appendages bearing rows of hairs to perform important functions like capturing food or molecules from the surrounding fluid, swimming or flying, or creating currents for ventilation or feeding. All of these functions depend on how the appendages interact with the surrounding water or air. When an organism moves a hair-bearing structure through the surrounding fluid, does the fluid move through the gaps between hairs rather than around the perimeter of the whole array? How is appendage performance of different functions affected by whether they act like leaky sieves or like solid paddles?

I first became interested in this question as a graduate student while trying to understand how benthic suspension feeders captured their microscopic prey from the water flowing through their filtering structures, which at that time were described as sieves that only caught particles larger than the gaps between neighboring tentacles or setae. Starting with a student project in Steve Vogel's biofluiddynamics class, Dan Rubenstein and I used engineering filtration theory to analyze different physical mechanisms of particle capture by the cylindrical setae or tentacles of filter-feeding organisms and how each mechanism was affected by the morphology of the filter and speed of fluid flow (Rubenstein & Koehl 1977). We learned that filters can capture particles smaller

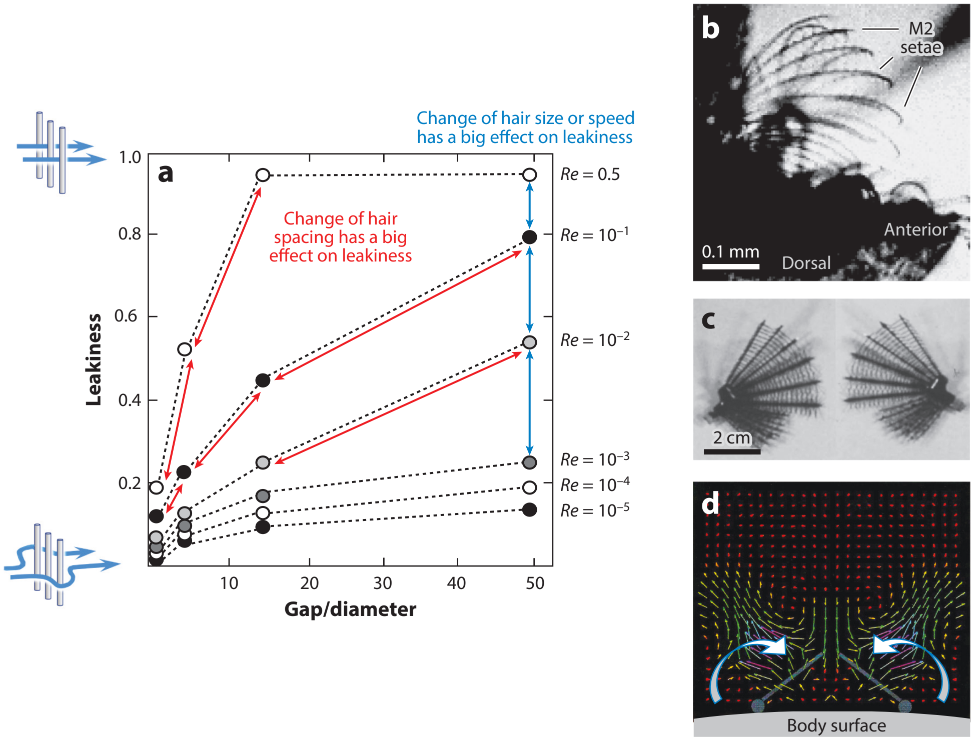


Figure 5

Hairy little legs. (*a*) The leakiness (volume per time of fluid moving through the gap between neighboring cylinders divided by the volume per time of fluid that would move through a space of equal area if the cylinders were not there) calculated for a finite-width row of cylinders, plotted as a function of the ratio of the width of the gap between neighboring cylinders to the diameter of the cylinders. Each line represents a different Reynolds number (*Re*). Panel adapted from Cheer & Koehl (1987) with permission from Elsevier. (*b*) Frame of one of our early high-speed ciné films (made with G. Paffenhofer) of a copepod, *Centropages velificatus*, viewed from its left side while it was flinging apart its second maxillae (M2s) during capture of an algal cell. The hairs (setae) bear smaller hairs (setules). During the fling, the *Re* of the setae is low enough that the arrays of setae on the M2s have low leakiness and behave like paddles, drawing water between them as they move apart. (*c*) Dynamically scaled physical models of the M2s of *C. velificatus*. (*d*) Velocity vectors measured by particle image velocimetry (PIV) around the model M2s (diagrammed as *gray lines* hinged to the body at the *gray circles*) of *C. velificatus* during the squeeze phase of particle capture, as they are moving toward each other and the body of the copepod (motion shown by *white arrows*). The model is viewed from the anterior end of the copepod. During the squeeze, the M2s move more rapidly than during the fling, so the *Re* is high enough that water flows between the setae. The leakiness of the M2s during the squeeze is enhanced by interaction with the body surface. Thus, during the squeeze, the algal cell is carried toward the mouth and the excess water around it is pushed away between the setae.

than the gaps between hairs. The theory suggested mechanisms by which biological filter feeders could be size selective and could change their size selectivity. Calanoid copepods are a critical link in ocean food webs, and their size-selective feeding on phytoplankton affects plankton community structure, so copepods provided a research system of ecologically important size-selective feeders to test our theory.

Copepods capture algal cells with their second maxillae (M2s), which bear long, hairlike setae (**Figure 5*b***). I worked with Rudi Strickler, who had developed an optical system to make high-speed movies of tiny copepods. We made movies of dye streams near copepods to visualize the water flow produced by their flapping appendages and were surprised to find that they do not strain phytoplankton out of the water as described in the literature. Instead, they flap four pairs of appendages to move water past themselves and fling their pair of M2s apart (**Figure 5*b***) to draw parcels of water containing algal cells toward their mouth (Koehl 1981, 1984b; Koehl & Strickler 1981; Childress et al. 1987). The bristled appendages of the copepods behaved as solid paddles rather than open rakes. That set me off on a quest to figure out what determined the leakiness of an array of hairs.

The Reynolds number (*Re*) is the ratio of inertial to viscous forces for a flow situation ($Re = LU\rho/\mu$, where L is a linear dimension of an object, U is fluid velocity relative to the object, ρ is fluid density, and μ is fluid dynamic viscosity, its resistance to being sheared). Large organisms like us operate at high *Re*, where inertial forces predominate, disturbances to a fluid persist, and flow is turbulent. In contrast, microscopic organisms operate at low *Re*, where viscous forces determine how the fluid moves, so flow is laminar and the boundary layer of fluid stuck to and moving with a body is large relative to the size of the body. If we use the diameter of setae on copepod appendages as L, we find that they operate at low *Re*. Filtration theory was developed for infinite arrays of cylinders operating at low *Re*, but copepod appendages bear a finite number of hairs, so water can flow around the hair array as well as through it.

My first postdoc was Angela Cheer, a mathematician who developed a model of flow around rows of cylinders of finite width. We used her model to explore the effects of hair diameter, spacing, and speed on the leakiness of the array (Cheer & Koehl 1987) (**Figure 5*a***). Changing either size (L) or speed (U) changes the *Re*. We found that at very low *Re*, hair arrays operate like solid paddles (little fluid moves between the hairs), and hair speed, size, and spacing can vary with little consequence for performance. In contrast, at *Re* between 10^{-2} and 0.5, changes in hair speed, size, and spacing have a big effect on leakiness, and appendages can transition between being paddles and sieves. Do organisms employ this leakiness transition when they use hairy appendages to catch prey or molecules from the water around them?

When the fluid dynamics of a complex three-dimensional appendage using non-steady-state kinematics is studied, constructing a dynamically scaled physical model that operates at the same *Re* as the real appendage can be a faster process than developing a computational model (Koehl 2003). An example of how we used such models to figure out how copepods capture algal cells is illustrated in **Figure 5*b–d*** (Koehl 2004). Using both physical and mathematical models, we have discovered more basic rules about flow through hair arrays (Koehl 1992, 1995, 1996a, 1998, 2001, 2004; Loudon et al. 1994). Hair length only affects leakiness at $Re < 10^{-2}$. Increasing the number of hairs in a row enhances leakiness if $Re > 1$ but decreases leakiness if $Re < 1$. The motion of a row of hairs toward a wall increases leakiness (**Figure 5*d***), but motion along a wall only increases leakiness at $Re < 10$. Therefore, as *Re* changes, there can be transitions not only in leakiness but also in which behaviors and morphological features can affect leakiness. With these rules in mind, we moved on from studying particle capture to investigating molecule capture by hairy appendages.

The first step in processing olfactory information, before neural filtering, is physical capture of odor molecules from the surrounding fluid. Many animals capture odors from turbulent currents or wind using antennae bearing chemosensory hairs. We focused on the fluid dynamics of molecule capture by crustacean olfactory antennules bearing such hairs. Using high-speed kinematic analyses and morphometrics of the olfactory antennules of lobsters, crabs, and stomatopods, coupled with experiments using dynamically scaled physical models, we analyzed what happens when these animals flick their antennules (Koehl 1996a, 2001, 2011; Mead et al. 1999, 2003; Mead & Koehl 2000; Goldman & Koehl 2001; Koehl et al. 2001; Stacey et al. 2002; Reidenbach et al. 2008; Schuech et al. 2011; Waldrop et al. 2015a,b; Waldrop & Koehl 2016). Antennules flick at the critical velocity at which their arrays of chemosensory hairs become leaky, so water flows between the hairs into the array. Then the antennules use a slow return stroke and the hair array becomes unleaky, trapping the water sample long enough for odor molecules to diffuse to the chemosensory hairs. The next flick sweeps out the old water sample and replaces it with a new one. Thus, these animals take discrete water samples in space and time (effectively sniffing the water). We found that antennule flicking has a profound effect on the flux of molecules to the chemosensory hairs, and we measured how flicking antennules physically filter the information (spatial and temporal distributions of concentration) in turbulent odor plumes as the animals navigate in the environment (Koehl et al. 2001, Mead et al. 2003, Koehl 2006, Reidenbach & Koehl 2011).

2.4. Lessons Learned About Research

Seeking answers to questions like those above has taught me a few basic lessons:

1. When data tells us our ideas are wrong, celebrate. The unexpected is what teaches us something new.
2. To understand how organisms work, go outside and study them in their natural habitats on the spatial and temporal scales of *their* lives. Field studies of the physical environment, ecological interactions, and life history strategies of organisms reveal which aspects of their performance are important to their success in different habitats.
3. Physical and mathematical models enable us to explore parameter space and perform experiments that are not possible with living organisms. A mathematical theory is a quantitative expression of how we think something works, showing us which parameters are important. Experiments can test predictions of theory or point the way to new theory. By leapfrogging our way between mathematical models and empirical studies, we move toward a better understanding of how organisms function.

3. SOME OF MY HISTORY, AND THINGS I LEARNED ALONG THE WAY

3.1. Art and Science

My father was a physics professor and my mother an artist. When the family watched sunsets, my father explained the physics of why the sky turned red, and my mother told us to look for the purple shadows and golden highlights on the clouds. My parents had rigid views about gender roles, so while my brother was encouraged to become a doctor, I was sent to college to major in art (a suitable pursuit for a woman). I went to Gettysburg College, a small liberal arts college where we were required to take courses in different fields to gain a well-rounded education. Even though I was an art major, I had to take a science course, so I took biology. I was fascinated by natural forms (bones, shells, seaweeds, spiders) and motion (running, flying, ocean waves), and I used them in my drawings and paintings. In biology class, I discovered that it was much more satisfying for me to understand how those forms worked than simply to use them to make images in my artwork. Thus, midway through college, I switched from art to majoring in biology. My parents were horrified because science was not a viable path for a woman.

Because I did not envision scientific research as a career path, I had the freedom to take science courses for the sheer pleasure of learning about how the natural world worked. A week-long field trip to the coast for my Invertebrate Zoology class (taught by Robert Barnes, who wrote the textbook on invertebrates that was in use at many universities at that time) introduced me to the idea that we cannot understand how organisms work unless we go outdoors and learn how they function in their natural habitats. That field trip convinced me that marine biology was my real love. During my senior year, I realized that I did not want to stop learning about biology, so I decided to go to graduate school.

Many people think that art and science are opposite pursuits. Having studied both art and science, I have come to see features they share, so I am not surprised that artists like da Vinci and Michelangelo were also scientists and engineers. Both artists and scientists are keen observers of the world, although we scientists have tools that let us see beyond what the naked eye of an artist can perceive. Both also deal with abstraction, so we represent the essence of what is important about something, rather than all its details. In some lectures, I show a slide with Matisse's paper cutout *Les Bêtes de la Mer* side by side with a page of equations from one of my scientific papers. Both are abstractions of the same thing: hydrodynamic forces on marine organisms of different shapes, and how they deform in those forces. I collaborated with an artist to produce a book of images and words that also showed these same principles (Koehl & Rosenfeld 2006). It is often said that art conveys emotion, while science is cold and devoid of feelings. The scientific method is designed to produce objective studies, and scientific papers convey data and theories without emotion, but the very act of doing science involves the passion of seeking answers, the excitement as the results roll in, the frustration when we are stumped, and the camaraderie of collaborators on a quest together.

3.2. The Importance of Mentors

I have been lucky to have had wonderful mentors from the time I started graduate school until today. What makes a good mentor? Here is what my mentors did that was so valuable to me. They taught me how to find and think about the relevant background for a scientific issue and to identify the gaps in our knowledge, rather than just handing me a question. They probed why I thought certain questions were exciting or important. They were critical sounding boards for my ideas, but let me explore and bark up some wrong trees while giving me the sense that they had confidence in me. Mentors showed me technical tools and approaches, discussing what they can and cannot do. They also introduced me to interesting people and sent me to conferences in diverse fields to get me thinking in new ways. Perhaps the most important feature shared by all my mentors was that each of them had a contagious delight in the process of exploring how the world works. They were role models who knew that scientific research can be fun. I strive to be a mentor like they were to me, but they are tough acts to follow.

As a beginning graduate student in the Department of Zoology at Duke University, I was a teaching assistant in Introductory Biology, taught by Steve Vogel. He gave a mind-bending lecture about size and scaling, where I first learned that the physical world experienced by microorganisms is very different from what we big creatures encounter. I was so excited by the lecture that I asked Vogel if I could be his graduate student. He told me the size lecture was actually Steve Wainwright's and advised me to wait until Wainwright returned from sabbatical before choosing a major professor. I became Wainwright's student, but I am grateful to Vogel for teaching an inspiring course in biofluiddynamics and for happily showing me how to build my own research equipment and flow tanks, tutoring me in how to solder and use a lathe. I still teach my students Vogel's formula for deciding whether a research project should be done: Maximize $(PV)/t$, where P is the probability of success, V is the value of the discovery to be made, and t is the time required to do the project.

Steve Wainwright (**Figure 6*a***) studied the mechanical design of diverse organisms. He shared my love of biological form and of art and was a sculptor in his spare time. He had studied at Cambridge and used the British-style tutorial to introduce his graduate students to biomechanics and critical thinking, so we met with him every week to discuss research publications and to turn in our review papers about specific subjects. We learned to write by responding to his extensive comments written all over our papers with colorful felt-tipped pens. We dreaded his "crystal ball

Figure 6

Some of my mentors. (*a*) Steve Wainwright (*left*), who taught me about biomechanics and the crystal ball question, and Bob Paine (*right*), who taught me about ecology and fieldwork, laugh with me at my wedding. Photo by P. Morse. (*b*) I learned a great deal from the expertise of and questions posed by my collaborators, students, postdocs, and lab assistants. Much of my research would not have been possible without the collaboration of Tim Cooper, a mechanical engineer who was my lab technician for many years. (*c*) My peer mentors are a group of women scientists who have been meeting every other week for over 40 years to help each other solve career-related challenges. Sitting on Einstein's lap at the National Academy of Sciences, where four of us have been elected members, are (*top*, *in red*) Carol Gross and (*bottom*, *left to right*) Mimi Koehl, Christine Guthrie, Suzanne McKee, Ellen Daniell, Judith Klinman, and Helen Wittmer; also in the group is Beth Burnside (not pictured here). Photo by S. Gross.

question," but it taught us how to identify experiments and research questions worth pursuing. I would tell him about an experiment I wanted to conduct, and he would say, "If I had a crystal ball and could tell you the result, so what?" I would slink away and think about it and return to him to say, "If I get this result, then we can answer the following question. . . ." He would again say, "If I had a crystal ball and could answer that question, so what?" We would repeat this process until I could stand up to him and say, "Answering this question is important for the following reasons. . . ," and then he would say, "Great! Go do it." I have used the crystal ball question on myself and students throughout my career.

Studying organisms in their habitats is a critical aspect of my research. I learned how to do fieldwork from Bob Paine (**Figure 6*a***). My dissertation research was on the mechanical design of hydrostatic skeletons. When I was searching for the right organisms to study, Bob gave a seminar at Duke about the ecology of wave-swept rocky shores. He mentioned sea anemones that sat on the bottom of surge channels catching mussels ripped off the shore by waves. I wondered how water balloons could withstand crashing surf and decided that sea anemones were the hydrostats I wanted to study. When I discussed this with Wainwright, he suggested that I write to Bob to ask if I could accompany him and his students to their field sites to see if studying those anemones was feasible. Had I taken an ecology course and known that Bob was a famous giant in his field, I would have been afraid to contact him. Fortunately, he was open-minded and generously invited this nascent biomechanist to join his field trips. I learned ecology during discussions around the campfire with Bob and his students. By working with them at their field sites, I learned about the natural history and environment of rocky shores and how to do rigorous field experiments. I accompanied them on a research expedition along the Chilean coast, and I continued to work with Bob and his crew on Tatoosh Island for many years (**Figures 1** and **2*a***).

I have had great mentors since graduate school. When I was a postdoc with Richard Strathmann at Friday Harbor Laboratories, I learned larval ecology, but also the importance of evolutionary biology to understanding the form and function of organisms. When I was a postdoc at the University of York in England, John Currey taught me how to study the mechanics of biomaterials and how their behavior is determined by their microarchitecture. When I was a beginning assistant professor at the University of California, Berkeley, a more senior faculty member, George Oster, coached me on how to navigate in such a large, complex university and on what I should accomplish to get tenure. George did biomathematical modeling, and he convinced me that my research could benefit from collaboration with mathematicians. He encouraged me to attend Gordon Research Conferences on biomathematics, where I could pitch my questions to people who have since become great collaborators. This led to sabbatical invitations to the Centre for Mathematical Biology at the University of Oxford and to the Newton Institute at the University of Cambridge, and to my work over many years at the Santa Fe Institute. In addition, I have been taught about many interesting organisms, valuable techniques, and intriguing ideas by my collaborators from different fields. Most of all, I have learned from my students, postdocs, and lab technicians (**Figure 6*b***). They are biologists, engineers, ecologists, physicists, and mathematicians who have brought a wonderful array of diverse expertise to my lab, and who have asked many interesting questions that kept me thinking and learning.

The mentoring that enabled me to survive as a university professor came from a small group of women who were facing the same challenges as I was. When I started my career, there were very few women in science. A handful of young women scientists in the San Francisco area found each other and formed what is now called a peer mentoring group (**Figure 6*c***). We have been meeting every other week for over 40 years. Our meetings follow procedures developed by therapists to keep group discussions safe and productive, as detailed in a book by group member Ellen Daniell (2006), where she also describes things we learned over the years about managing work–life balance and coping with the hurdles at universities, research institutes, and biotechnology companies. Although the challenges we face have evolved with each career stage, we know we can turn to each other for support and ideas about how to proceed. We have helped other scientists start such peer-mentoring groups and are happy to do so today.

My take-home message about mentoring is that we each need many mentors. The person who can help us learn to teach may not be the best writing coach, the person who can craft effective grant proposals may not be the one who knows how to give dynamite talks, and the person who can teach us how to navigate the politics of a university may not be the mentor to turn to for technical guidance with experiments.

3.3. Women in Science, an Underrepresented Group Back When I Started

When I started my career, there were very few women in science. There were no women biology professors at Gettysburg College or in the Department of Zoology at Duke. There were only four women graduate students in my entering class in zoology, and I was the only one to complete a PhD.

Given my love of marine biology, I thought I wanted to become a biological oceanographer. I was excited to be a Summer Student Fellow at the Woods Hole Oceanographic Institution (WHOI). I had to rent a room in town by myself, while all the men got to live together in a dorm. I must admit that sometimes I snuck into the dorm lounge to share a beer and discussions with the guys. Back then, women were not allowed on oceanographic research ships, so I had to build my research setup and then sweet-talk one of the guys to run my experiments for me while the ship was at sea. I felt like the wife of a whaling captain standing on the WHOI dock waving my hanky at the menfolk as they set out to sea. That is why I am not an oceanographer. Fortunately, just a few years later, women were allowed on ships, and many are now leading oceanographers.

I had many experiences when I was interviewing for faculty positions and starting out as an assistant professor that are amusing in retrospect, but that made me feel like a real outsider at the time. During one job interview, the desk clerk at the hotel accused me of being a call girl when I asked for the key to my room. He said the room was registered to Dr. Koehl, who was obviously a man because women are not doctors. I learned about the stereotype of a woman scientist when I arrived at the airport to begin my job interview at Berkeley. The faculty member meeting me in the arrival hall was holding a sign that said “Dr. Koehl.” When I walked up to him and introduced myself, he kept looking over my shoulder at the other arriving passengers. I tried reintroducing myself, and he finally looked at me, blinked a few times, and said, “Oh. You’re Dr. Koehl? I was expecting someone as ugly as a mud fence and wearing sensible shoes.”

I published using my initials rather than my full name because I did not want potentially biased reviewers to know I was a woman. That meant I was invited, based on my published work, to give talks at conferences and universities by people who did not realize I was female. At one meeting where I was the only woman, I was assigned a male roommate in the housing (after a lot of snickers and some last-minute scrambling, the situation was rectified). After one of my lectures, a fellow came up to the podium to tell me about some relevant papers by Koehl that I should read. When I explained that I was Koehl, he said, “No you’re not. Koehl is an old guy with a beard.” I loved the idea that I wrote like someone with a beard. At a Dahlem Conference in Berlin, the men at the meeting assumed that the young woman with the German “Koehl” on her nametag was a member of the support staff and kept asking me to xerox things or bring them coffee.

I hope that sharing my experience of being a woman in science back when there were so few of us will provide useful hints for members of other underrepresented groups that are making their way into the scientific community now. Peer mentoring from that small group of other women outsiders like me was crucial. So was a sense of humor, and so was the boxing glove a friend gave me that I used to punch my filing cabinet when things just got too frustrating to bear. I chose to play by the existing rules and to work harder than everyone else so I could survive in the system. My hope was that if I succeeded, maybe I could convince the “old boys’ club” that women could do science too, and maybe I could inspire some girls to give science a try. Others may choose to spend time and effort to change the system, and that is important too. My bioassay that women in science have come a long way is that now there are so many women at scientific conferences that I miss talks because I am stuck in long lines waiting for the ladies’ room.

3.4. Interdisciplinary Research

My research in ecological and evolutionary biomechanics is interdisciplinary. I use approaches from physics and engineering to work out how the morphologies of organisms affect their performance in natural habitats of activities that affect their ecological roles and fitness. When you work between disciplines, you are an outsider in each of the fields you are straddling. On my first (unsuccessful) interview for a faculty position in a biology department, one of the professors interviewing me told me that I should go apply for jobs in engineering departments and quit wasting his time. My first several (unsuccessful) grant proposals to the biological oceanography section of the National Science Foundation to study mechanisms of suspension feeding got a number of reviews that simply said, “This is not oceanography.” It is also a challenge to figure out which scientific journals will consider papers that do not sit squarely in the discipline they cover.

Being an outsider meant that I did not fit into the sessions at scientific meetings. As a graduate student, the first talk I gave at an oceanography meeting was about hydrodynamic forces on wave-swept intertidal animals, a poor fit for a meeting that focused mainly on larger-scale ocean processes. When I gave my talk, the only people in the room were the guy running the session, the projectionist, and Dick Barber, a Duke professor who made it his business to support all the Duke students at the meeting by attending our presentations. At biomechanics meetings, I talked about kelp or copepods, while everyone else focused on medical or sports biomechanics of humans. At zoology meetings, I reported on hydrodynamics in sessions about animal behavior. At fluid dynamics meetings, I lectured about how larvae land on wave-swept coral reefs, while others presented mathematical models of isotropic turbulence. A good thing about participating in meetings where I did not belong is that I learned about different approaches I could apply in my research. I also met a few people willing to collaborate, teaching me how to use their techniques to answer my oddball questions.

Fortunately, things have changed since those early days as more organismal biologists work at the interface between biology and physics, and as more biomechanists understand the importance of ecology to their studies (Koehl 2023). There is now a Division of Comparative Biomechanics in the Society for Integrative and Comparative Biology, and there is an international Small-Scale Ocean Biophysics group. There are even textbooks about comparative biomechanics (Vogel 2013) and ecological biomechanics (Denny 2016). My interdisciplinary work has now been recognized by the very same scientific societies that ran the conferences where I spoke to empty rooms when I was starting out (Borelli Award, American Society of Biomechanics, for “outstanding career accomplishment”; Rachel Carson Award, American Geophysical Union, for “cutting-edge ocean science”; Muybridge Award, the “highest honor” of the International Society of Biomechanics; and Fellow of the American Physical Society).

Sometimes people working in a field are hostile when you use an approach from a different discipline to address their questions. For example, when I first spoke at a conference about the fluid dynamic mechanisms copepods use to catch algal cells, one eminent zooplankton oceanographer told me that Newton’s laws might apply to my species of copepod, but they did not apply to his, while another senior figure ordered me to give him one good reason why any agency should fund my useless research. In spite of all that early sneering and rejection, this work later won the Martin Award for research that “created a paradigm shift in an area of aquatic sciences” from the Association for the Sciences of Limnology and Oceanography.

Although interdisciplinary researchers face the sorts of challenges I have mentioned, there is a delicious freedom that comes with being an outsider working between fields. If nobody has thought of or cares about the questions you are asking, then you are not competing with a crowd to get to the finish line first. You are free to explore wherever the discoveries lead you. The same is true if you are using some wacky approach from another field to address a question that everyone else is studying in the standard way. Sometimes other researchers become interested in our interdisciplinary questions, which is incredibly gratifying. However, when an area of inquiry gets crowded, I leave for more open spaces.

For a while, the National Science Foundation funded Integrative Graduate Education and Research Traineeship (IGERT) grants to develop graduate programs in interdisciplinary research. The engineering and biology professors in our IGERT program at Berkeley discussed how we should train students in interdisciplinary research. We did not want our interdisciplinary students to be superficial jacks of all trades but masters of none, so we agreed that each student must become an expert within one discipline and earn their PhD in that department. In addition, our graduate students worked together in interdisciplinary research teams (Full et al. 2015) to learn from each other three important aspects of each other's fields: (*a*) the techniques and approaches that each field can offer and the types of problems they can address; (*b*) the language used in each field, so that effective cross-disciplinary communication is not lost in a sea of jargon (e.g., the term stress means something very different to engineers, physiologists, and psychologists); and (*c*) the exciting unanswered questions in each field. Few people can be enticed to participate in a collaboration if their expertise serves only as a handmaiden to answer someone else's question. Successful interdisciplinary collaborations have something interesting for every participant.

3.5. Dyslexia: How We See the World

I got to know Jack Horner (of dinosaur fame) at meetings of MacArthur ("genius grant") Fellows. When he was visiting Berkeley to work in our Museum of Paleontology, we went to lunch. After we had walked to the restaurant and ordered, he asked me if I was dyslexic. He said he was dyslexic, and he rattled off a list of things he had watched me do that he recognized, like the way I gave directions (I can't tell right from left, but north and south are easy) and held my butter knife under each line of the menu to read it. Nobody talked about dyslexia when I was a schoolkid, and I had never been tested. I shrugged it off and didn't think about it again until the campus changed the locks on our lab doors to number pads. I could not manage to punch the numbers correctly, so I was locked out of my own lab. When I asked to have a metal key for my lab door and the building manager refused, I remembered what Jack had said. I tried arguing that I could not operate the keypad because I was dyslexic. I was told that if I got tested and was certified as "learning disabled," then the Americans with Disabilities Act would apply to me, and I could get a key to my lab as an accommodation. So, in my mid-forties I spent eight hours taking tests for dyslexia, and was told at the end of it that I had the biggest discrepancy they had ever seen between my dismal symbol perception and processing scores and my IQ scores. I was so happy. I got a key to my lab, and many things about my life started to make sense.

I set out to learn more about dyslexia, and found out that, although dyslexics have trouble reading, many of us are better than normal people at visualizing how three-dimensional shapes and processes change with time, at reasoning in multiple dimensions and identifying patterns, and at seeing connections between different perspectives and fields of knowledge (reviewed in Taylor & Vestergaard 2022). Jack got me involved with Dyslexic Advantage, an organization that works to enable children with dyslexia to take advantage of their strengths rather than dwell on their disability. I expected successful dyslexic engineers, architects, and sculptors to be involved with that group, but was surprised to meet dyslexic hedge fund managers as well. Each of them told me some version of how they "see" the shape of evolving financial trends. My love of fluid dynamics and of biological forms and motion makes sense to me now. I was given a lemon (dyslexia), but I learned to make lemonade (research in biomechanics and biofluiddynamics).

Learning I was dyslexic helped me understand some of my quirks and things that happened in the past. The letters *b*, *d*, and *p* are all the same to me, just different views of the same object. I can't tell the difference between long words that start and end with the same letters (e.g., street signs in Honolulu are all the same "K. . .a" to me). I scramble phone numbers and cannot see spelling errors. When I read, I have to hold a ruler under each line of text; otherwise, the white spaces that meander down the page draw my eyes off the row of little black marks that represent words, and I get hopelessly lost. I read painfully slowly. In college, I struggled in literature and history classes because I couldn't complete the long reading assignments in time. In science classes, I couldn't read the textbooks or memorize the information before exams, but I discovered that I could use principles I had learned in lecture to figure out the answers to test questions instead. Before my diagnosis, I thought I was incompetent because grading student papers and reviewing journal manuscripts and grant proposals ate up a huge amount of my time, while my colleagues could whip through those tasks quickly.

We each view the world differently and think about it in our own unique ways. This was made clear to me when my husband and I did a research project together about transport and mixing across benthic communities in different marine habitats (Koehl et al. 1993, 1997; Koehl & Powell 1994). I am lucky to be married to another nerd, Thomas (Zack) Powell, a particle physicist turned oceanographer. We enjoy the same weird things (like vortices on evening news weather maps), we are supportive of each other's careers, and we understand why we each work all the time. We thought we might see more of each other if we did a research project together. Unfortunately, Zack kept getting frustrated when he wrote equations to explain to me what he thought was going on, and I would instead plot a graph or draw pictures of how I thought things worked. In exasperation he would sigh, "That is exactly what I have been trying to tell you!" I now understand that he thinks in equations, whereas I think in graphs and pictures because I am dyslexic.

4. REFLECTIONS

My life in marine science has been a life outside—both literally, because of all the field research I do, and figuratively, because my work does not fit neatly in a single discipline, because women were intruders in the halls of science when I started, and because I see the world differently as a dyslexic. Although being an outsider poses many challenges, it also brings great freedom of inquiry. The guidance of diverse mentors made it all possible.

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The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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