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WHEN DOES MORPHOLOGY MATTER?

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ABSTRACT

The performance of an organism is the crucial link between its phenotype and its ecological success. When does an organism's morphology affect its performance? Quantitative mechanistic analyses of how function depends on biological form have shown that the relationship between morphology and performance can be nonlinear, context-dependent, and sometimes surprising. In some cases, small changes in morphology or simple changes in size can lead to novel functions, while in other cases changes in form can occur without performance consequences. Furthermore, the effect of a specific change in morphology can depend on the size, shape, stiffness, or habitat of an organism. Likewise, a particular change in posture or behavior can produce opposite effects when performed by bodies with different morphologies. These mechanistic studies not only reveal potential misconceptions that can arise from the descriptive statistical analyses often used in ecological and evolutionary research, but they also show how new functions, and novel consequences of changes in morphology, can arise simply as the result of changes in size or habitat. Such organismal-level mechanistic research can be used in concert with other tools to gain insights about issues in ecology (e.g. foraging, competition, disturbance, keystone species, functional groups) and evolution (e.g. adaptation, interpretation of fossils, and origin of novelty).

INTRODUCTION

The biological literature abounds with qualitative arguments about the selective advantages of particular morphological traits; more recently such qualitative arguments have been replaced by quantitative correlations between structural or performance characteristics of organisms and their fitness or ecological role.

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Such qualitative or statistical statements are often made without a mechanistic understanding of how the morphological traits affect performance. Nonetheless, the performance of an organism is recognized as the crucial link between its phenotype and its ecological success (e.g. 7, 8, 20, 45, 91, 104, 198, 228, 229).

The purpose of this article is to draw together for ecologists and evolutionary biologists examples of the nonlinear, context-dependent, and sometimes surprising relationships between the morphology and performance of organisms. These nonintuitive effects, which have been revealed by mechanistic organismal-level investigations, are often missed in descriptive statistical or phylogenetic studies that use morphological or performance data. I have two goals in reviewing this information: One is to warn about the misconceptions that can arise from descriptive statistical studies that are blind to mechanism, and the other is to point out ways in which such organismal-level mechanistic information can be used to gain insights about issues in ecology (e.g. foraging, competition, disturbance, keystone species, functional groups) and evolution (e.g. adaptation, interpretation of fossils, and origin of novelty).

Some Definitions

I define the *morphology* of an organism as its structure on any level of organization from molecular to organismal, and I define *performance* as a measure of ability to carry out a specific function. Although some authors (8, 45) consider behavioral and physiological traits as morphology, I view them here as functions (although this distinction can sometimes be blurred—75). Furthermore, while some authors (8, 45) define performance as a measure of whole-organism capacity, I also consider performance of parts of organisms (e.g. appendages, enzymes). A *function* of a structure is simply a function the structure is capable of doing [i.e. *fundamental niche* sensu, (198); *performance* sensu, (63)], whereas a *role* of a structure is a use to which the structure is put by an organism in a given environment [i.e. *realized niche* sensu, (98); *behavior* sensu, (63)] (20, 60, 134). How well a structure performs a role (such as food-gathering) is often assumed to affect the fitness of the organism (e.g. 60, 134), although fitness may depend most on the performance of rare life-or-death roles (such as escape maneuvers) (198). *Fitness* is the number of zygotes or surviving offspring, corrected for rate of population growth, produced by an individual during its lifetime (45).

The Biomechanical Approach to Studying Effects of Morphology on Performance

There is a long history of research on the relationship between biological structure and function (reviewed by 137, 158, 229, 232, 234). One approach to functional morphology is biomechanics, the application of quantitative engineering techniques to study how organisms perform mechanical functions and interact with their physical environments. Biomechanists are concerned with elucidating the basic physical rules governing how biological structures operate, identifying physical constraints on what organisms can do, evaluating which structural characteristics affect performance, and analyzing the mechanisms responsible for the effects of morphological differences on performance (e.g. 3, 4, 35, 40, 44, 45, 54, 60, 104, 131, 134, 153, 166, 185, 198, 224, 226, 228, 230, 234). Although some biomechanists have been accused of assuming that natural selection has led to the morphologies being studied (e.g. 232), many of us simply focus on the mechanisms by which form affects function without making inferences about evolutionary origin. In addition to being a legitimate field on its own, biomechanics has also served as the handmaiden of other disciplines (232), providing useful tools for studying questions in ecology as well as in evolutionary biology and paleontology.

EXAMPLES OF SURPRISES THAT ORGANISMAL-LEVEL MECHANISTIC STUDIES REVEAL ABOUT HOW MORPHOLOGY AFFECTS PERFORMANCE

Many quantitative studies of the effects of morphology on performance are reviewed in biomechanics books (e.g. 3, 35, 40, 153, 166, 185, 224, 226, 230). My purpose here is not to summarize the field, but rather to focus on examples of the nonlinear and context-dependent ways in which performance depends on structure. After introducing basic types of nonlinear relationships between structure and function, I describe two examples of how the relationship between morphology and performance can be surprising (fluid dynamics of little hairs, and effects of body shape and texture on drag). I then discuss in more general terms the categories of nonintuitive effects of morphology on performance that we should keep in mind when using morphological data to address ecological or evolutionary questions.

Overview of Nonlinear Effects of Morphology on Performance

If the quantitative relationship between a measure of performance and a measure of morphology is nonlinear, then there are ranges of the morphological parameter where modifications of structure make little difference, and other ranges where small morphological changes can have large consequences. For example, an asymptotic curve is shown in Figure 1a: increasing the number of receptor sites on a cell increases the rate at which it adsorbs molecules when receptor numbers are low, but offers little improvement when receptor numbers are high (17).

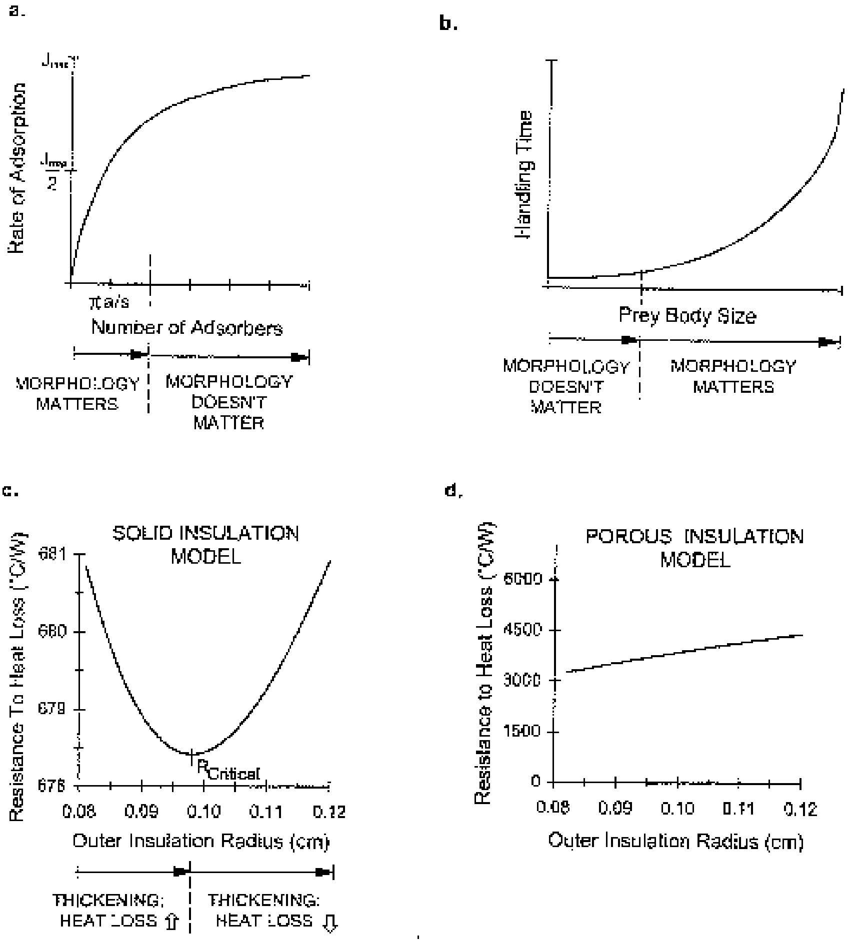

Figure 1 Examples of the relationship between performance (*y* axis) and morphology (*x* axis). (*a*) Rate of molecule adsorption (molecules per time, where J_{max} = number of molecules per time captured by a sphere whose entire surface is adsorbing receptor sites) of a spherical cell, plotted as a function of the number of adsorbing receptor sites on the cell (where a = radius of cell, s = radius of a single receptor site). [Curve calculated using equation 8 in (17)]. (*b*) Handling time for a predator to eat a prey organism (the higher the value, the better the performance of the prey), plotted as a function of prey body size. [Redrawn by digitizing one of the curves in Figure 6.3 of (46)]. (c) Resistance to heat loss by a heated cylindrical body (diameter = 0.16 cm) surrounded by a layer of solid insulation, plotted as a function of the outer radius of the body plus insulation. Resistance was calculated for heat loss by conduction through the insulation, and by free convection and radiation from the outer surface of the insulation. [Redrawn by digitizing the total resistance curve in Figure 2 of (192)]. (*d*) Resistance to heat loss by the same heated cylindrical body, but with porous insulation. [Redrawn by digitizing the free-convection curve in Figure 6 of (192)].

An example of an exponential curve is shown in Figure 1b: Differences in the size of small prey have little effect on predator handling time and hence on the prey's likelihood of being eaten, whereas differences in body size between larger prey can have a big effect on the danger of becoming a meal (46). [Of course, once prey become large enough that they escape in size from predation (179), differences in size once again become unimportant to the risk of being eaten.] Many aspects of mechanical performance also have exponential relationships to morphological features [e.g. deflection of a bending beam bearing a given load $\propto$ length^3; weight borne by a skeleton $\propto$ body volume $\propto$ length^3; volume flow rate through a pipe $\propto$ diameter^4; and many others described in e.g. (2, 3, 154, 166, 226, 230)]. Thus, performance of functions like skeletal support should be insensitive to structural variation at small size but very sensitive to morphological changes at large size.

If the relationship between performance and a morphological variable goes through a maximum or a minimum (Figure 1c), then the effect of increasing the morphological variable reverses once it passes a critical value. We are used to trying to relate such maxima and minima to the peaks and troughs in adaptive landscapes (e.g. 58, 104). In addition, we might also consider that passing through such an inflection point represents the acquisition of a novel consequence for a particlar type of morphological change. For example, if a heated body is surrounded by a non-heat-producing layer (e.g. extracellular cuticle, mucus, or fur), thickening that layer enhances the rate of heat loss from the body until a critical outer radius is reached, above which further thickening of the layer reduces heat loss (Figure 1c) (192). This critical radius concept from heat transfer physics was used to argue that naked baby mammals and birds would lose heat faster if they had feathers or fur (12), but calculations by Porter et al (192) showed the critical radius to be too small to be relevant (Figure 1c). Furthermore, when the non-heat-producing layer surrounding the body was assumed to be porous (like feathers or fur containing air spaces), the calculated resistance to heat loss was much greater than when the insulating layer was assumed to be solid (Figure 1d) (192). This example illustrates the importance of doing quantitative assessments of how morphology affects performance and of using biologically relevant assumptions in calculations.

Now, armed with the idea that the effect of morphology on performance is sometimes nonlinear, I provide some examples of various types of surprising relationships between morphology and performance.

Performance of Hairy Little Legs

Many animals from different phyla use appendages bearing arrays of hairs to perform important biological functions such as suspension-feeding, gas exchange, olfaction, mechanoreception, and swimming or flying (Figure 2a-e).

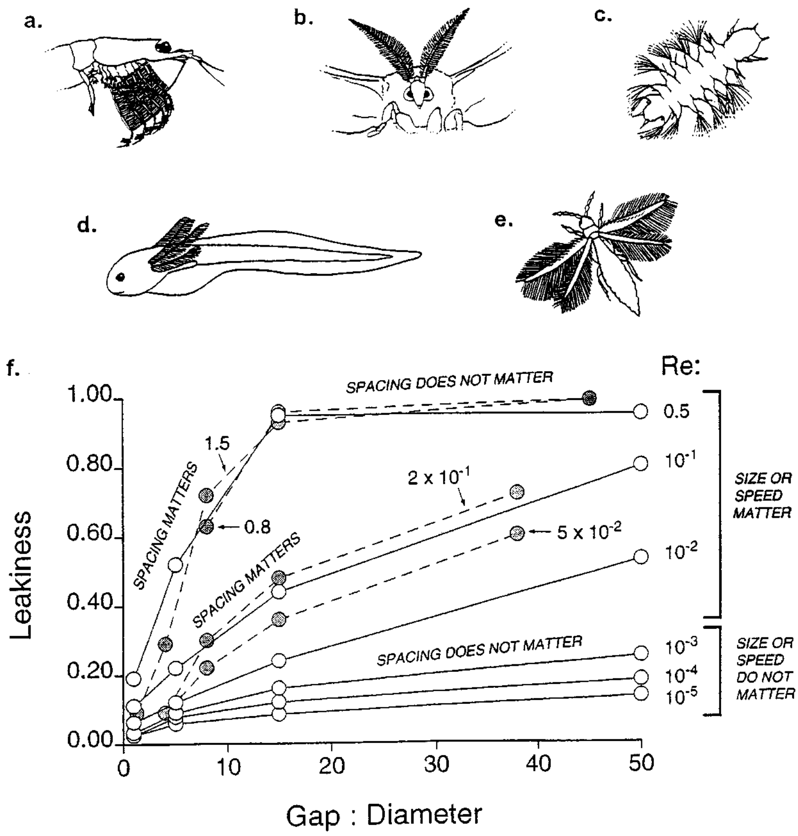

Figure 2 Examples of hair-bearing appendages that serve different functions: (*a*) suspension-feeding legs of a euphausid, Phylum Arthropoda; (*b*) olfactory antenna of a male moth, Phylum Arthropoda; (*c*) swimming parapodia of a nereid larva, Phylum Annelida; (*d*) external gills of a larval African lungfish, Phylum Chordata; wings of a thrips, Phylum Arthropoda. (*e*) Plot of leakiness (volume of fluid flowing through the gap between adjacent hairs divided by the volume of fluid that would flow through a space of that width if the hairs were not there) as a function of gap:diameter ratio of neighboring hairs. Open circles and solid lines represent leakiness calculated using the model of Cheer & Koehl (30). Grey circles and dashed lines represent leakiness measured during towing experiments with comb-like physical models of Hansen & Tiselius (78). Each line represents a different Re, as indicated by the numbers near the lines. [Redrawn from Figures 1 and 3 in (119)].

To carry out any of these functions, an array of hairs must interact with the water or air around it; thus, to understand how appendage morphology affects performance we must analyze the fluid dynamics of arrays of hairs.

Reynolds number (Re) represents the relative importance of inertial to viscous forces for a particular flow situation ($\mathrm{Re} = LU/\nu$) where L is a linear dimension such as hair diameter, U is fluid velocity relative to the hair, and ν is kinematic viscosity of the fluid (226). At high Re's (e.g. large, rapidly moving structures), inertial forces predominate, so flow is messy and turbulent, whereas at low Re's (e.g. small, slowly moving structures), viscosity damps out disturbances in the fluid, hence flow is smooth and orderly. When fluid flows past a solid surface, the fluid in contact with the surface does not slip relative to the surface, and a velocity gradient (boundary layer) develops between the surface and the freestream flow. At low Re's, boundary layers are thick relative to the dimensions of the structure.

Most of the types of hairs listed above operate at Re's of order 10^{-5} to 10 (119). If the layers of fluid stuck to and moving with the hairs in an array are thick relative to the gaps between hairs, little fluid leaks through the array. Since performance of the functions listed above depends on the leakiness of hair-bearing appendages (reviewed in 119, 120), the effects of hair spacing and Re (size or speed) on leakiness have been explored using mathematical and physical models (Figure 2f) (29, 30, 78, 118–120). Although hairy appendages look like sieves, they are not always leaky: at $\mathrm{Re} < 10^{-3}$, so little fluid leaks through the gaps between neighboring hairs that arrays of hairs function like paddles; in contrast, at Re's $> 10^{-2}$, fluid flows readily between the hairs and arrays behave like leaky filters. Another surprising discovery is that at Re's $< 10^{-3}$, changes in morphology (hair diameter or spacing) or behavior (speed) have little effect on leakiness (i.e. there is permission for morphological and behavioral diversity without performance consequences), whereas at Re's of 10^{-2} to 1, changes in size or speed can have a big effect on leakiness. Moreover, at Re's of 10^{-2} to 10^{-1}, decreasing gap width reduces leakiness, whereas at $\mathrm{Re} = 1$, changes in hair spacing affect leakiness only when hairs are quite close together. The effect of a morphological change can also reverse at a critical Re: adding more hairs to an array reduces leakiness if $\mathrm{Re} < 1$, but has the opposite effect if $\mathrm{Re} > 1$ (D Abdullah, personal communication; 119). The leakiness of an array is increased when it moves near a wall (such as the body surface) if $\mathrm{Re} < 10^{-2}$ (146)—thus the behavior that can alter leakiness changes as an animal grows (i.e. altering appendage distance from the body when $\mathrm{Re} < 10^{-2}$, versus changing appendage speed when $\mathrm{Re} > 10^{-2}$).

The hairy feeding appendages (second maxillae, M2's) of calanoid copepods (Figure 3) provide a biological example of the consequences of these physical

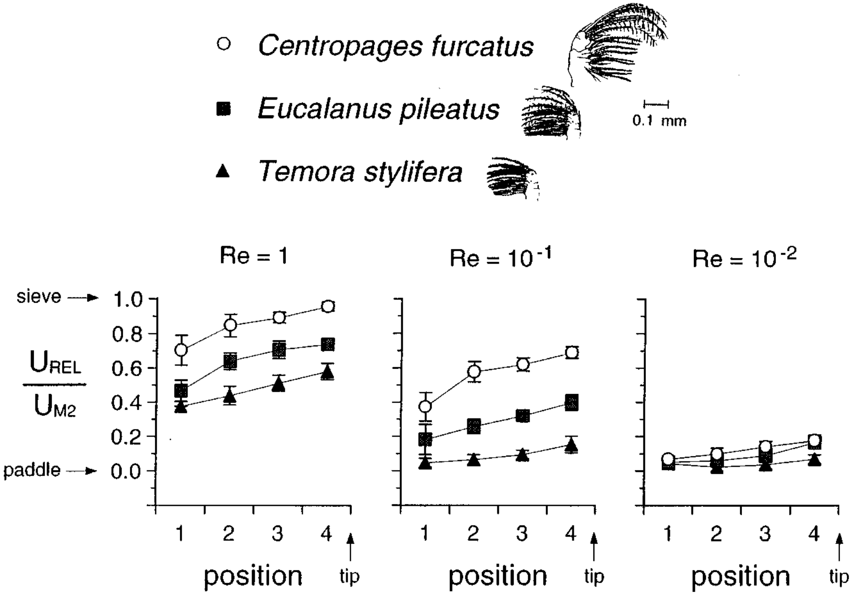

Figure 3 Fluid movement through dynamically scaled physical models of the M2's (pictured at the top) of *C. furcatus* (open circles), *E. pileatus* (grey squares), and *T. stylifera* (black triangles). The mean values of U_{REL}/U_{M2} (where U_{REL} is the absolute value of the fluid velocity relative to the M2, and U_{M2} is the velocity of the M2) for each section along the length of the model (section 1 near base, 4 near tip) are plotted for models run at a Re of 1 (*left graph*), 10^{-1} (*middle graph*), and 10^{-2} (*right graph*). Error bars indicate one standard deviation ($N = 3$ to 12). The lower the value of U_{REL}/U_{M2}, the less leaky (i.e. the more paddle-like) the M2. Note that the coarseness of the mesh of the M2's affects leakiness at Re's of 1 and 10^{-1}, but not at 10^{-2}. *C. furcatus* operate their M2's at Re $\simeq$ 1 (at which the M2's are sieve-like), *T. stylifera* at Re $\simeq 10^{-2}$ (at which the M2's are paddle-like), and *E. pileatus* at Re $\simeq 10^{-2}$ to 10^{-1} (a range in which the M2 leakiness varies). (Redrawn from Figure 14 in 119).

rules (118, 119). Copepods capture single-celled algae by flinging apart their pair of M2's and then squeezing them back together (114). Some species (e.g. *Centropage typicus*) that have coarsely meshed M2's, whose setae (hairs) operate at Re = 1, have leaky M2's and filter their food from the water during the squeeze; in contrast, other species (e.g. *Temora stylifera*) that have finely meshed, slowly moving M2's, whose setae operate at Re = 10^{-2}, have paddle-like M2's that capture food by drawing a parcel of water containing an algal cell toward the mouth during the fling. Thus, even though their M2 feeding motions look qualitatively similar, the physical mechanisms by which these two copepods capture food are different because they operate at Re's above and below the transition from paddle to sieve. Some copepods (e.g. *Eucalanus pileatus*) are plastic in their behavior and can switch their M2 speed, and thus leakiness, for different functions; note that only organisms operating in this transitional Re range can alter their leakiness by this means.

Thus, quantitative study of mechanism has revealed the conditions under which permission exists for morphological diversity of hairy appendages with little consequence to performance, versus conditions under which simple changes in hair speed, size, or spacing can lead to novel physical mechanisms of operation.

Effects of Body Shape and Texture on Fluid Dynamic Drag

Drag is the hydrodynamic force tending to push a body in the direction of fluid movement relative to the body (explained in e.g. 25, 40, 113, 226), hence drag tends to dislodge sessile organisms and to resist the motion of swimming, flying, and sinking creatures. At low Re's, drag is due to skin friction (the viscous resistance of the fluid in the boundary layer around the body to being sheared as the fluid moves past the body), so greater wetted area leads to higher skin friction. At high Re's drag is due to skin friction plus form drag (the pressure difference across the body due to the formation of a wake on the downstream side of the body). The bigger the wake, the higher the form drag; hence any morphological feature that moves the flow separation point (i.e. the place the wake starts to form) rearward along a body reduces drag at high Re. The drag coefficient (C_D) is a dimensionless measure of the drag-inducing effect of body shape.

Streamlining (putting a long, tapered end on the downstream side of a body) is one familiar way to reduce form drag, although the increased area raises skin friction. For large, fast organisms operating at high Re, streamlining reduces the net drag, but for small, slow organisms at low Re, streamlining increases drag. For example, C_D's of globose ammonoid shells are lower than C_D's of flat, streamlined shells at $Re < 100$, but the reverse is true for larger shells at higher Re (95). Similarly, drag on small ($Re = 1$ to 10) benthic stream invertebrates is lowered if their shape becomes more hemispherical, but is lowered on larger animals ($Re = 1000$) if they become more flattened (216). Nonetheless, most lotic invertebrates do not change shape as they grow, having streamlined profiles even when small (215). However, even though streamlining doesn't work when small stream insects are exposed to slow currents, flat body shapes do reduce hydrodynamic-resistance to their higher-Re escape maneuvers (34). For animals like these insects that can cross a Re transition by changing their speed, the Re of the activity that has the greatest impact on fitness (e.g. escape) appears to be the Re for which the body shape is drag-reducing.

Another morphological feature that has different effects on drag at different Re's is surface roughness (25, 109, 223, 226) (Figure 4). As the Re of a bluff body increases (i.e. as a nonstreamlined organism grows or moves more rapidly), C$_D$ drops when flow in the boundary layer along the body's surface suddenly becomes turbulent and carries the separation point rearward, producing a smaller wake and lower form drag. At Re's below point A in Figure 4, surface texture is buried in the boundary layer and has no effect on drag, whereas at very high Re's surface bumps can protrude through the boundary layer and increase skin friction drag. However, surface roughness can trip the boundary layer to go turbulent at a lower Re than for a smooth body. Thus, there is a range of Re's (between A and B, Figure 4) in which a bumpy surface reduces drag on a bluff body. The shape of an organism's body affects whether or not this drag-reducing effect of bumpy skin occurs: Net drag on streamlined bodies is simply increased by surface texture once the critical Re is reached (A, Figure 4). The verrucae on sea anemones do not affect drag because the animals' Re's are below the transition Re (109). In contrast, tubercles increase

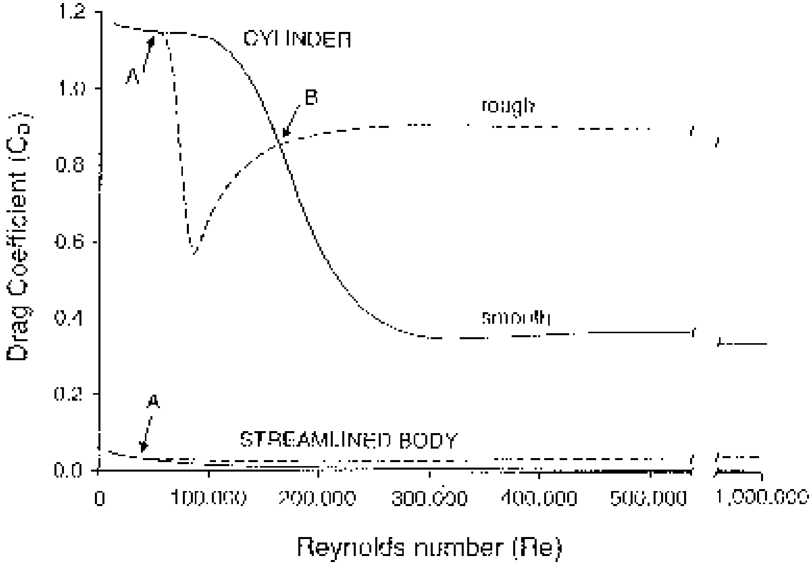

Figure 4 Plot of drag coefficient (C$_D = 2\,D/\{\rho S U^2\}$, where D = drag, ρ = fluid density, S = plan area of body, U = fluid velocity relative to body) as a function of Reynolds number (Re $= \rho UL/\mu$, where L = linear dimension of body, μ = dynamic viscosity of fluid) for a cylinder at right angles to the flow, and for a streamlined body (note that both axes of graph are log scales). The solid lines indicate bodies with smooth surfaces, and the dashed lines indicate bodies with rough surfaces. *A* indicates the onset of turbulence in the boundary layer, and *B* indicates the point beyond which roughness increases drag on the cylinder. (Redrawn using data digitized from Figure 5.8 in 226).

the drag on a swordfish's high-Re sword, but induce a turbulent boundary layer over the fish's body such that net drag on the whole fish is reduced (25, 223).

Both the examples described above (leakiness of hair-bearing appendages and drag on bodies) involve structures moving relative to the surrounding air or water, and both illustrate that the performance consequences of particular morphological characters depend on Re. I now discuss in more general terms the categories of nonintuitive effects of morphology on performance that we should keep in mind when using morphological data to address ecological or evolutionary questions.

Morphology Does Not Affect Performance

When the morphology of a structure does not affect the performance of some function, there is permission for diversity of form and for assumption of other functions.

MORPHOLOGICAL FEATURES THAT HAVE LITTLE EFFECT ON PERFORMANCE

Denny (42) found that lift is more important than drag in removing limpets from the substratum; thus features affecting only drag do not influence limpet performance at resisting ambient flow. Limpets show high diversity in the shell characters that affect drag.

Organisms that swim by flapping appendages at high Re can generate thrust to propel the body by using either drag or lift on the appendages. Vogel (226) noted that appendage shape has a big influence on lift-based swimming performance but makes little difference to drag-based propulsion, and he thus predicted that multifunctional appendages should use drag to generate thrust. Indeed, the walking appendages of polychaetes, ducks, muskrats, and freshwater turtles all use drag-based propulsion during swimming, whereas the lift-based flippers of sea turtles serve poorly as walking legs.

In some cases only part of a structure is critical to performance, so there is permission for diversity of form of the noncritical regions of the structure. For example, the morphology of the petiole and basal lobes of a tree leaf determine how easily it rolls up in the wind, but the diversity of form of the rest of the leaf does not affect performance of this drag-reducing rolling (225, 226). Butterflies bask in the sun to warm up, using their wings as solar panels. Dark wings absorb more heat, but since most of the heat transferred to the body comes from the basal region of a wing, there is permission for the rest of the wing to sport defensive or cryptic color patterns without interfering with thermoregulatory ability (235). At Re's where surface roughness affects drag, bumps on the anterior and widest regions of a body are very important to drag, whereas texture on the posterior region of a body makes little difference (25).

PERMISSION FOR DIVERSITY OF MORPHOLOGY AND KINEMATICS AT SMALL SIZE As mentioned above, skeletal structures should be insensitive to structural variation at small size. Indeed, there is variability in the ossification of bones (i.e. in their material stiffness—35; in very small salamanders—77). Similarly, the tiny stalks of the fruiting bodies of cellular slime molds show simple geometric scaling, in contrast to large biological columns (e.g. tree trunks, leg bones) that as they grow must become disproportionately wide relative to their length to support body weight (22, 154).

There are also biofluiddynamic functions whose performance is insensitive to morphology or kinematics at small size, such as the hair-spacing and surface roughness examples described above. Many small free-swimming organisms create feeding currents past themselves by flapping appendages. Calculation of the scanning currents produced by different types of appendage motions shows that for each technique, the energy cost per volume of water scanned changes very little if animals depart from optimal appendage kinematics (although which scanning technique is most efficient depends on the size of an animal's target zone—the distance at which it can perceive and capture prey) (31).

Another example of permission for kinematic diversity at small size is provided by basilisk lizards, which run on the surface of water (66, 67). The force to support the lizard's body during this sort of locomotion is provided by an upward impulse as the foot slaps onto the water surface, followed by an upward impulse as the foot strokes down into the water. Comparison of water-surface running by basilisks of different sizes revealed that small animals, which have the capacity to generate a large force surplus relative to their body weight, varied their kinematics considerably without performance consequences, whereas larger animals, which can generate barely enough force to support their weight, were constrained to a narrow range of leg and foot motions to run successfully on water. Indeed, in the field juveniles often run on water simply to move to another sunning spot, whereas adults venture onto the water only under duress.

Small Changes in Morphology or Simple Changes in Size Lead to Novel Functions

We should expect transitions in hydrodynamic or aerodynamic function as organisms grow or clades evolve through different Re ranges. Examples of such transitions were described above for the leakiness of hairy appendages and the drag on streamlined or rough bodies. Other examples can be found in ontogenetic studies of swimming. For instance, as brine shrimp larvae get bigger, even though the flapping motion of their appendages does not change, their propulsive mechanism switches from drag-based rowing at low Re to inertial swimming at higher Re (241, 242). Similarly, larval fish switch from drag-based swimming at low Re to inertial propulsion when they grow to higher Re (14, 176), and intermittent swimming becomes more energetically advantageous as the importance of viscous force declines at higher Re (237). Another example is provided by scallops, which swim by jet propulsion by squirting water out of the mantle cavity while clapping their shells together. Very small juvenile scallops cannot use this inertial mode of locomotion effectively and are sedentary; larger scallops can jet, and once at Re > 3000, they can also use lift to get up off the substratum; however, when very large they become poor swimmers again, as their shells grow too heavy relative to the thrust they can generate (36, 147).

Functional transitions accompanying size changes can also be found for organisms moving through air. For example, wing shapes that optimize gliding performance of plant seeds or animals depend on Re: short, wide wings are better at small size, whereas long, narrow wings enhance gliding at large size (51). An example of how isometric size changes in the absence of shape changes have the potential to generate novel functions is provided by the experiments of Kingsolver & Koehl (105, 107) that tested the aerodynamic and thermoregulatory consequences of changes in the length of protowings on models of fossil insects. At small body size, short thoracic protowings can improve thermoregulatory performance, although they have negligible effect on aerodynamic gliding, parachuting, or turning performance; in contrast, protowings of the same relative length on a larger insect can improve aerodynamic performance. This illustrates that it is physically possible for a simple increase in body size to cause a novel function (i.e. a solar panel can become a wing) without requiring the invention of a novel structure. (However, whether protowings served these aerodynamic or thermoregulatory roles in early insects is just as speculative as other feasible hypotheses, like sexual signaling, gas exchange, or skimming along the surface of a body of water.)

Another example of a functional switch accompanying a simple continuous change in morphology is provided by the chitinous exoskeleton (perisarc) of hydroid colonies (92) (Figure 5a). If bent too far, perisarc kinks like a beer can, damaging the tissue inside (Figure 5b). Perisarc, which has annulated regions and internodes, is thickened with time. Tissue damage from kinking is worse in annulated regions than internodes when perisarc is thin near the growing tips of colonies, but as the perisarc is thickened, these roles reverse and the annulated regions provide protection from damage when the colony is subjected to large bends (Figure 5c,d).

Dimensionless numbers, such as Re, that express the relative importance of various physical factors affecting a process, can provide us with hints of other places to look for functional shifts. For example, Froude number (gravity

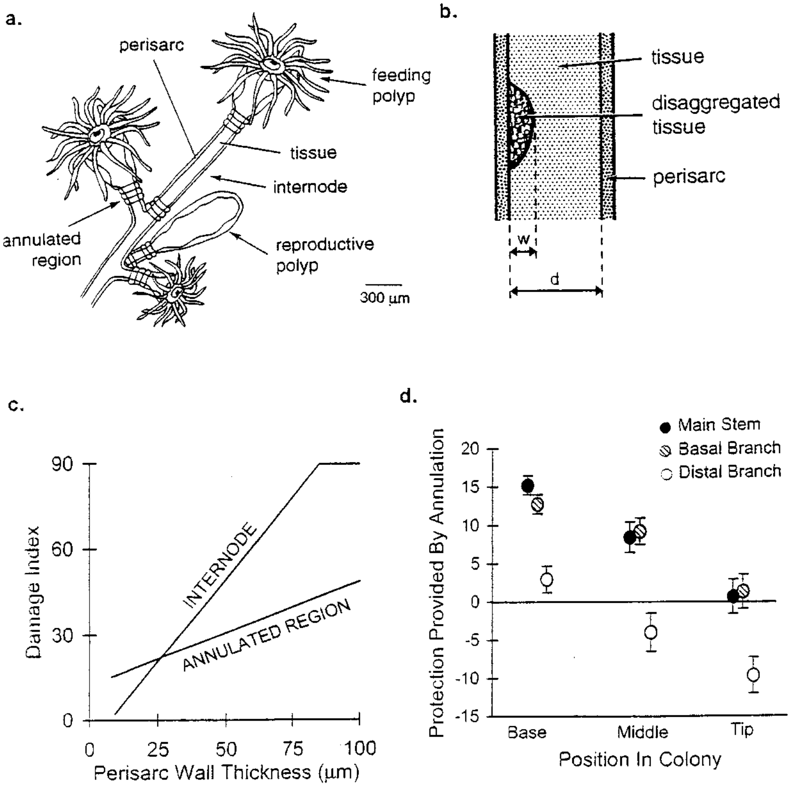

Figure 5 Perisarc of the hydroid *Obelia longissima*: (*a*) Diagram of the tip of a branch of a colony, showing the annulated and internode regions of the perisarc. (*b*) Diagram of the tissue damage (disaggregated tissue) caused by perisarc kinking when bent (w = width of damaged tissue, d = diameter of tissue inside the perisarc). (*c*) Damage index (arcsin w/d), plotted as a function of perisarc wall thickness for internode and annulated regions. The internode line levels off at a damage index of 90, indicating complete tissue damage. [Redrawn by digitizing the regression lines in Figure 7, Chapter 1, of (92).] (*d*) Index of protection from damage (a measure of the protection of soft tissue afforded by the presence of annulations in the perisarc, given by the difference between tissue damage in the internode region and tissue damage in the annulated region) for different regions of hydroid colonies. Error bars = 95% confidence intervals (n = 93 per group). Positive values indicate that annulations protect from damage, whereas negative values indicate that annulations make damage worse. [Redrawn using data digitized from Figure 8, Chapter 1, of (92).]

relative to inertia) is a good predictor of gait changes in pedestrian locomotion (e.g. 5), while reduced frequency (accelerational relative to steady-state flow) indicates the importance of nonsteady-state mechanisms of generating lift and thrust in swimming or flying (e.g. 37), and Péclet number (fluid convection relative to molecular diffusion) indicates the importance of bulk air or water movement in getting molecules to the surface of a collecting device such as a gill or olfactory antenna (120).

Effects of a Morphological Trait Depend on Other Characteristics of an Organism's Body

Single traits should not be studied in isolation (68), not only because multiple traits can affect a particular aspect of performance (e.g. 4), but also because both the magnitude and direction of the performance consequences of a particular morphological change can depend on other aspects of an organism's structure.

An example of the interactive effect of several traits on performance is provided by flying frogs, tree frogs that glide through the forest canopy and that have a unique suite of derived morphological characters, including enlarged hands and feet. An aerodynamic study using physical models of flying and nonflying frogs on which such characters could be modified one at a time revealed that the effects of the flyer traits on aerodynamic performance were nonadditive (48). For example, all the flyer traits occurring together improved turning performance significantly more than expected from the sum of their individual effects. However, for certain aspects of aerodynamic performance, the effect of the co-occurrence of flyer traits depended on body size: Gliding performance was improved more than expected only for small frogs, whereas parachuting performance was improved less than expected only for large frogs.

Performance of a structure at one level of organization can depend on morphology at another level of organization. In the following examples, the deformability of a structure (which depends on tissue microarchitecture and molecular composition—e.g. 224, 230) can affect the consequences of variation in gross morphology. While Lauder (132) has proposed a phylogenetic method to examine the independence of different levels of organization during evolution, mechanistic studies like those cited below reveal the physical reasons that performance depends on the interaction of different levels of structure.

Flexible sessile organisms experience lower drag forces than do rigid ones of the same shape because the deformable organisms are passively blown into more streamlined shapes (e.g. 109, 115, 225, 226). Flexibility also determines whether or not body shape even affects flow forces. Because of passive streamlining, the drag coefficients of various species of floppy intertidal algae are similar when water velocities are high enough to cause damage, even though they have very different shapes (28). In contrast, blade shape does affect drag for the less flexible blades of bull kelp (121). Denny (42) has suggested that once a lineage has become sufficiently flexible, shape may be removed from further selection by drag.

Flexibility can also determine the consequences of growth for organisms of a given shape, as illustrated by model studies of planar sessile organisms (122). If a planar rigid organism (e.g. a plating hydrocoral) lengthens in a wave-swept habitat, the hydrodynamic force it bears rises, whereas if a very flexible organism lengthens (e.g. a floppy alga that can move back and forth with the flow), the force on its holdfast remains low (Figure 6). However, a flexible organism in waves must grow to a critical size before it can benefit from "going with the flow": A floppy creature can move with the flow only until it reaches the end of its tether, at which point the water moves past it and it must bear the hydrodynamic force (115). Thus, algae that are short relative to the distance the water travels in a wave before it reverses direction do experience an increase in force as they grow (64). Furthermore, an organism of intermediate flexural stiffness can deflect enough to move with the flow only after the organism has become sufficiently long (deflection of a cantilever $\propto$ length^3), so as it grows, the force rises, then plateaus, and then decreases (Figure 6). Flexibility also determines which sort of flow habitat is most mechanically stressful: For rigid organisms, waves produce larger forces than do unidirectional currents of the

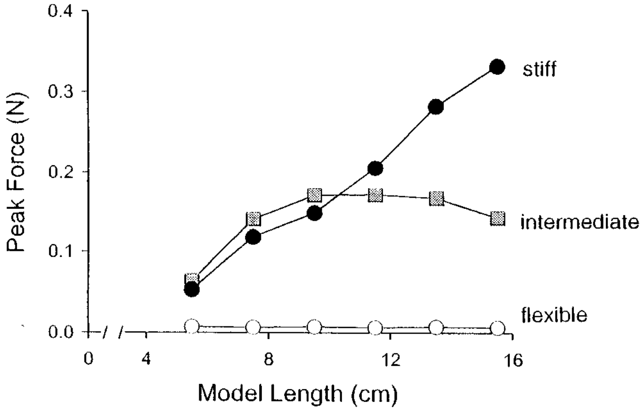

Figure 6 Peak hydrodynamic force measured on models of planar benthic organisms of different stiffnesses exposed to oscillatory flow in a wave tank, plotted as a function of model length. Error bars, which represent 95% confidence intervals ($n = 5$ per point), are smaller than the symbols used on the graph. The models maintained constant width and thickness as they "grew" (M Koehl, T Hunter, and J Jed, unpublished data).

same peak velocity, whereas the opposite is true for flexible organisms (122). Another example of the consequences of flexibility is provided by protozoans that locomote by undulating flagella that bear hairs (mastigonemes). Both fluid dynamical analysis (52) and observations of swimming protozoans (86) show that when mastigonemes are stiff, protozoans swim in the same direction as the direction of wave propagation along the flagellum, whereas when mastigonemes are flexible, the organisms swim in the opposite direction (as do protozoans without mastigonemes).

Effects of a Morphological Trait Depend on Habitat

The performance of an organism is meaningful only in the context of the environment in which the organism lives (e.g. 63, 74, 109). The following examples illustrate not only that changes in habitat can have profound effects on performance, but also that the consequences of a morphological modification can depend on the environment.

One environmental variable whose effect on performance has received much attention from biologists is temperature. Temperature is perhaps the most commonly used abscissa on graphs in physiology books, and the effects of temperature on important biological and ecological processes such as locomotor performance, predator-prey interactions and foraging strategies, development rate and life history patterns, and habitat use are well documented (e.g. 32, 63, 81, 82, 87, 90, 189–191). Other more subtle effects of temperature on mechanical performance include changes in the mechanical properties (such as stiffness, resilience, strength, and toughness) of biological tissues (e.g. 110, 112, 224, 230), and a shift in the Reynolds number of aquatic organisms [due to changes in kinematic viscosity, which nearly doubles between 0° and 20°C, as well as to changes in the rate of movement of some species (e.g. 187, 188, 215, 226, 245)]. Therefore, the body speeds and sizes at which Re-dependent functional shifts occur depends on habitat temperature. Obviously the temperature changes that accompany diurnal and seasonal cycles, climate shifts, microhabitat changes, and species range extensions can have profound effects on the performance of organisms with given morphologies.

Another obvious feature of the physical environment that can have enormous mechanical and physiological consequences is whether an organism is surrounded by air or water. The transition between aquatic and terrestrial habitats has been made in the evolution of many lineages. This transition between water and air is also made during the ontogeny of some species (e.g. with aquatic larvae and terrestrial adults) and is made daily by intertidal organisms and by animals that locomote between the two habitats (e.g. littoral crabs, diving birds). The consequences to performance of moving between these two media are reviewed by Denny (41) and Vogel (226).

Benthic marine organisms are exposed to unidirectional currents at some sites, but to waves (oscillatory flow with high accelerations) at others. The morphology of a spawning animal in waves does not affect gamete dispersal (123), although it does in gentler unidirectional flow (221). Similarly, streamlining works only if flow direction can be predicted, and hence it is ineffective at wavy sites (42, 109). Furthermore, the consequences of growth to a stiff organism's risk of dislodgment by hydrodynamic forces are different in the two types of habitats. The attachment strength of a sessile organism depends on holdfast or foot area ($\propto L^2$), and the drag and lift it must withstand in unidirectional flow depends on plan area ($\propto L^2$), whereas the acceleration reaction force in waves depends on body volume ($\propto L^3$) (e.g. 40, 109). Therefore, wave-swept organisms have a physical constraint on body size not experienced by creatures in steady currents (43).

Flow conditions in the environment affect the feeding performance of many aquatic animals that make their living by filtering small organisms and particles from the surrounding water. For example, ambient flow velocity affects not only the volume of water per time that a passive benthic suspension feeder can process for food and the amount of particulate material stirred up in the water (e.g. 171), but the velocity also determines the efficiency (proportion of encountered particles that are captured) and the size-selectivity of a filter of a given morphology (e.g. 204, 209). In addition, the turbulence (random fluctuations in velocity) of the flow can alter feeding performance of both planktonic (e.g. 151, 203, 210) and benthic (e.g. 183) suspension feeders. However, whether turbulence enhances or inhibits feeding rate depends on the morphology, swimming mode, and physical capture mechanism(s) used by an organism (209, 210).

An organism's performance can depend on the morphology of its neighbors. For example, the structure of canopies of terrestrial plants, or of aquatic sessile animals or macrophytes, affects the microclimate that they and the other organisms living among them encounter, often buffering them from fluctuations and extremes in environmental conditions (e.g. 56, 109, 115, 121, 157, 244). Similarly, the arrangement of individuals in aggregations of sessile benthic invertebrates, such as tubiculous phoronids and polychaetes, can affect the feeding and spawning performance of individuals within the aggregation (100, 101, 220, 221). Whether neighbors improve or harm the performance of a benthic animal depends on morphology. For example, the feeding performance of encrusting bryozoans is enhanced by upstream neighbors (but only if ambient flow is fast), whereas that of arborescent forms is reduced (172–174). Furthermore, physical constraints on organisms in aggregations can sometimes be different from those on solitary individuals: e.g. sea palm kelp in dense stands can support their crowns of blades on slimmer, taller stipes without buckling because they lean on their neighbors (85).

Another example of how habitat can alter the effect of a morphological feature on performance is provided by arboreal lizards. The effect of leg length on sprint speed depends on the diameter of the branch on which an animal runs (145).

Consequences of Behavior Depend on Morphology

I define behavior as an action taken by an organism, ranging from simple kinematics or assumption of a posture to complex interactions with other organisms. The consequences of a particular behavior can depend on the morphology of the organism. For example, the flying frogs described above take on a characteristic posture when airborne, with knees pulled forward and feet spread out laterally. Emerson & Koehl (47) discovered via model experiments that when frogs assume the flying posture, parachuting performance of the flyer morph improves whereas that of the nonflyer morph worsens; gliding performance worsens much more for the nonflyer than the flyer; and only turning performance improves for both morphs. Another example is provided by copepods (119): Although *E. pileatus* can alter the leakiness of their M2's by changing speed (from $\mathrm{Re} \simeq 10^{-2}$ to $\mathrm{Re} \simeq 10^{-1}$), if *T. stylifera* changed the speed of their more finely meshed M2's over the same Re range, leakiness would not change (Figure 2).

Functional Equivalency: "There's More Than One Way to Skin A Cat"

Evolutionary biologists (e.g. 58, 152) and ecologists (e.g. 219) have recognized that organisms can play the same role in a variety of ways. Studies of natural history and behavior reveal how different organisms perform the same task. For example, several taxa of lizards have the ability to dive into sand but utilize different techniques that involve distinct exaptations in each case (6); three species of snakes eat whiptail lizards, but use different methods to capture them (73); and a variety of mechanisms can play the same role in predator defense (50).

Biomechanical studies elucidate the physical principles underlying how different structures can serve the same mechanical function. For example, many animals in different phyla reinforce their soft tissues with mineral inclusions (e.g. spicules, sclerites, ossicles) whose bizarre shapes are so specific that they are used as taxonomic characters. Analysis of the mechanics of spicule-reinforced tissues as filled-polymer composite materials revealed that the stiffening effect of spicules depends on the surface area of the spicule-tissue interaction, but that the particular combination of spicule sizes, shapes, and numbers used to produce that surface area in a volume of tissue matters little to performance (112). Many other examples of functional equivalency can be found by considering the flexural stiffness (resistance to bending, EI) or torsional stiffness (resistance to twisting, τJ) of organisms. Both depend on the product of the elastic modulus (resistance to deformation, E in tension or τ in shear) of the tissues from which a structure is made, and to I or J, shape properties of the structure (proportional to radius^4) (e.g. 230). Thus, organisms can produce a flexible structure via the microarchitecture of their tissues or via the gross morphology of cross-sectional shape. Simple examples of both can be found among cnidarians: Flexible joints in some sea fans occur at regions of lower E (due to sclerite microarchitecture of the tissue) (162), whereas the bending joints in sea anemones (e.g. 111) and the torsional joints in sea pens (18) are due solely to local reductions in I or J.

Another example of functional equivalency is provided by the phenotypic plasticity of giant bull kelp in different water-flow habitats. As they grow, the kelp maintain the same ratio of stress (force per cross-sectional area) required to break the stipe (stem) to stress imposed on the stipe by hydrodynamic forces; they can do so by altering a variety of morphological traits: blade shape (affecting drag), stipe diameter (affecting stress), or stipe material properties (affecting strength) (102).

Summary: Nonlinear Context-Dependent Effects of Morphology on Performance

When does the morphology of an organism affect its performance? For structures that perform mechanical functions (e.g. skeletal support, locomotion, food capture), the relationships between morphological dimensions and measures of performance can be quantified using physical principles. Although many biomechanical studies have shown how particular aspects of performance are affected by defined changes in morphology, others have revealed cases in which changes in form can occur without performance consequences. Quantitative mechanistic studies of how function depends on form have also produced some intriguing surprises. For example, in some cases small changes in morphology or simple changes in size can lead to novel functions. Furthermore, the effect of a specific change in morphology can depend on the size, shape, stiffness, or habitat of an organism. Likewise, a particular change in posture or behavior can produce opposite effects when performed by bodies with different morphologies.

What implications do these findings have for ecologists and evolutionary biologists? I devote the rest of this review to pointing out ways in which quantitative mechanistic organismal-level research can be a useful tool in the arsenal of approaches for attacking ecological and evolutionary questions. I mention misconceptions that can arise by ignoring mechanism, but I also point out limitations of the mechanistic approach.

WHY SHOULD ECOLOGISTS CARE ABOUT THE MECHANISMS BY WHICH MORPHOLOGY AFFECTS PERFORMANCE?

Mechanistic Versus Phenomenological Approaches

Why should ecologists worry about how individual organisms work when they are studying populations, communities, or ecosystems? Both quantitative empirical studies and mathematical models of ecological processes can use either a phenomenological or a mechanistic approach (see historical review in 180). If we focus on phenomenological analysis of a population, community, or ecosystem, we are concerned *that* organisms perform certain processes (e.g. consume certain prey, overgrow neighbors, migrate, produce offspring) at defined rates, rather than worrying about the details of *how* they perform these activities. In contrast, mechanistic studies assume that particular processes at the organismal level are important in governing the behavior of a system at a larger level of organization, such as a population, community, or ecosystem. The pros and cons of phenomenological versus mechanistic approaches are reviewed in (116, 138, 194, 200, 206). Phenomenological models can be powerful tools for making short-term predictions about systems for which descriptive data are available. Although mechanistic models generally do not fit the data as well as phenomenological models and may be complicated and slow to provide answers, the development of mechanistic models can lead to an understanding of how a system works. A number of examples of how mechanistic studies have provided ecological insights are reviewed in (194, 206).

Organismal-level mechanistic information about how performance depends on morphology not only can reveal limitations to the interpretation of phenomenological data, they can also provide insights about the mechanisms underlying ecological processes.

Morphology as a Tool to Infer Function or Ecological Role: Usefulness and Problems of this Phenomenological Approach

BACKGROUND One common type of ecomorphological study is the statistical description of patterns of distribution of morphologies with aspects of the environment, community structure, or ecological roles organisms play (reviewed by 198, 199, 207). Such studies do not directly assess the functional meaning of morphological variables, but rather they assume that the ecological characteristics of a species can be inferred from its morphology (198). These descriptive studies are an effective way to reveal patterns that can guide further mechanistic research and that can aid in interpretation of fossil communities or poorly studied recent communities, but they are limited in their ability to establish cause and effect (88). The dangers of making spurious conclusions about causes using statistical tests based on descriptive models have been reviewed in 96.

IMPORTANCE OF MECHANISTIC INFORMATION The examples described above of the many ways in which the relationship between morphology and function can be surprising and complex should caution us against expecting simple correlations between structure and function to yield reliable predictions of performance. However, mechanistic studies can yield quantitative expressions of the basic physical rules governing how a type of biological structure operates. Such mechanistic equations can be powerful tools for predicting the effects of specific morphological parameters on defined aspects of function, even in cases where the effects are nonlinear and context-dependent.

Although there are certainly instances when the function of an organism has been inferred successfully from its structure alone (reviewed in 133, 228), many other cases exemplify the problems of trying to read function from morphology without the aid of mechanistic information (discussed by 59, 68). Anyone trying to infer function from morphology should be aware of the following potential problems when descriptive statistical studies are done without mechanistic analysis:

1. Statistical analyses may not reveal a connection between structure and function in cases for which the effects of morphology on performance are nonlinear, or for which different mechanisms can play similar roles, as illustrated by the examples described above.

2. Statistical studies can also fail to reveal a mechanistic relationship between a structural feature and performance if the feature studied is only one of several that affects the performance (4). For example, the adhesive force holding a tree frog to a surface is proportional to toepad area, but measures of angles of surfaces at which frogs slipped off (sticking performance) did not correlate with toepad area because sticking performance is also inversely related to a frog's weight (44). Similarly, frog leg length did not correlate with jumping distance (45), and fish streamlining did not correlate with swimming speed, because both aspects of performance also depend on muscle mass, arrangement, and power output (4).

3. Statistical studies can find correlations between morphological features and performance or fitness that are not causally related when other correlated

but unmeasured morphological variables are responsible for the performance differences assessed (7, 88, 96, 133, 134).

4. Greene (72), who found that morphology was a poor predictor of lizard diets, stressed the importance of the ecological context in which an organism operates. For example, function is difficult to infer from morphology when information is lacking about the trade-offs to which a structure is subjected if it serves more than one role (133). Furthermore, we may waste time correlating unimportant aspects of performance to morphological characters if we do not base our studies on natural history observations of what organisms actually do in the field (e.g. 73) and on quantification of physical conditions actually encountered by organisms in nature (e.g. 40, 42, 102, 109, 113, 190).

Organismal Mechanistic Studies Shed Light on Ecological Questions

BACKGROUND Processes acting at the level of individual organisms can determine the properties of populations, communities, and ecosystems (reviewed by 116, 198), hence the effects of morphology on performance can have important ecological consequences (e.g. 7, 16, 44, 53, 88, 206, 232). For example, biomechanical analyses reveal the mechanisms responsible for differences in susceptibility of intertidal organisms of various morphologies to removal by waves (e.g. 40, 42, 43, 109, 110, 113, 115, 124); such wave-induced disturbance is important in determining the structure of intertidal communities (e.g. 180, 181, 213). Biophysical analyses of heat and water exchange between animals and the environment reveal where and when particular species can be active, and hence such analyses point out morphological constraints on habitat use, on ecological interactions such as competition or predation (e.g. 71, 81, 82, 189–191), and on reproductive strategies (e.g. 103). Similarly, flight aerodynamics provides a mechanistic explanation for the patterns of foraging and competition by hummingbirds living at different altitudes (55), and of foraging and habitat use by bats of different morphologies (170), while swimming hydrodynamics and head biomechanics do so for fish (e.g. reviewed by 228, 236). Likewise, biophysical studies reveal physical constraints on the distribution and ecological interactions of plants of different morphologies (e.g. 166, 169). Mechanistic studies such as these also enhance theoretical ecology by elucidating factors that can be ignored versus those that must be included in mechanistic ecological models, by testing the assumptions of such models, and by providing realistic values for parameters used in model calculations (88, 116).

INSIGHTS PROVIDED BY RECOGNITION OF NONLINEAR, CONTEXT-DEPENDENT EFFECTS OF MORPHOLOGY ON PERFORMANCE Although the literature abounds with examples of how ecological studies are enriched by information about how organisms function, the nonlinear context-dependent effects of morphology on performance reviewed here may be especially useful in providing insights in the developing area of "context-dependent ecology." Evidence is accumulating (193, 219) that the ecological role played by a particular species, as well as its impact on community structure and ecosystem dynamics, depends on the ecological context (e.g. physical conditions, time since disturbance, ecosystem productivity).

Keystone species (e.g. 155, 156, 178), now defined as those species whose impact on a community or ecosystem is disproportionately large relative to their abundance or biomass (193), may not be dominant controlling agents in all parts of their range or at all times in the succession of a community (examples tabulated in 193). By weaving together organismal-level studies of how habitat affects performance with data about the ecological patterns characterizing situations in which a sometimes-keystone species does play a significant role, we may reveal the mechanisms responsible for the context-dependency of its importance. Although such studies have not, to my knowledge, been conducted yet, an example can be pieced together using information in the literature. Biomechanical analyses reveal that kelp with weak, deformable tissues can resist breakage by stretching like extensible shock absorbers when hit by waves. A context-dependent performance consequence of this mechanism (which depends on the microarchitecture of the tissue) is that such kelp are generally quite tough but can break easily if the long-duration waves that accompany storms stretch them beyond their limit (113, 114). A storm can clear an area of kelp when broken plants become entangled with their neighbors, which then also break (114, 124). An ecological study of the role of sea urchins in benthic communities showed that these animals are keystone grazers that control community composition in areas where kelp are absent, but not where kelp are present and they have plenty of drift algae to eat; storms can cause a community to convert from a kelp bed to a "barrens" controlled by urchin grazing (79). Thus, information about the organismal-level mechanical performance of kelp can shed light on the issue of when sea urchins are keystone species.

Functional groups (e.g. 218, 219) are suites of species that play equivalent roles in an ecosystem. Understanding the mechanisms responsible for functional equivalency at the organismal level may help us identify the circumstances under which one species can play the same ecological role as another. Again, an example can be pieced together from published studies about the convergence of ecological roles played by mussels (*Mytilus californianus*) on wave-swept rocky shores in Washington state and tunicates (*Pyura praeputialis*) in similar habitats in Chile (182). Both species are competitive dominants that can form mat-like monocultures of individuals attached to each other; interstices in these mats provide protected habitats for an assemblage of small organisms. The formation of holes ("patches") in these mats of competitive dominants is an important process affecting the diversity of the rocky shore community by providing space on the substratum to sessile species that would otherwise be out-competed (180, 181). A biomechanical analysis of the physical mechanisms by which patches are produced in mussel beds revealed that the same morphological features that lead to the ecological convergence of these mussels and tunicates also are responsible for patch initiation. The pressure difference between the slowly moving water in the interstices below the mats and the rapidly moving water in a breaking wave above the mats cause lift forces high enough to rip chunks of the mat away (39). Analysis of forces on individual mussels indicated that waves do not exert forces large enough to wash them away (39). Thus, evidence that the performance consequences of a given morphology are very different when in an aggregation than when isolated leads to this insight about why competitively dominant mat-forming intertidal species are also subject to patch formation.

Conclusions

Ecologists should care about the mechanisms by which morphology affects performance for two reasons. Knowledge of these mechanisms can reveal the limitations of interpretation of descriptive phenomenological information. Mechanistic information also can provide insights about processes affecting the structure of populations, communities, and ecosystems.

WHY SHOULD EVOLUTIONARY BIOLOGISTS CARE ABOUT THE MECHANISMS BY WHICH MORPHOLOGY AFFECTS PERFORMANCE?

Observations about the nonlinear context-dependent relationship between morphology and performance can provide insights about the evolution of biological structure to researchers using a variety of approaches: the externalists, who emphasize natural selection and the performance or fitness of different phenotypes in the environment (reviewed by 10, 229, 233); the paleontologists, who interpret fossil evidence about the history of evolution; and the internalists, who focus on the generation of form and on the ontogenetic mechanisms that might constrain phenotypic variation or produce novelty (reviewed by 10, 23, 65, 83, 161, 233).

Externalists: The Study of Adaptations

BACKGROUND Traditionally, when biologists noted correlations between particular morphological features and certain habitats or lifestyles of organisms, they referred to such features as adaptations (discussed by 20, 63). However, since Gould & Lewontin (68) harpooned this plausible-argument approach to identifying which traits are adaptations, the topic of adaptation has been contentious (144, 152). Today a morphological feature can strictly be called an adaptation only if it promotes the fitness of the organism and if it arose via natural selection for its present role (69). Although these requirements are difficult to satisfy, various research methodologies for identifying adaptations have been proposed (6–8, 16, 60, 62, 63, 73, 130, 131, 134, 136, 197, 198, 239). Many of these schemes incorporate the "morphology⟶performance⟶fitness" paradigm.

Arnold (7) formalized an emerging conceptual framework for studying the selective advantage of morphological features: The morphology of an organism can determine its performance, which in turn can affect fitness. This approach, which has become the "central paradigm in ecomorphology" (198), uses natural variation in populations to seek correlations between morphology and performance, and between performance and fitness (e.g. 7, 8, 63, 228). When this paradigm is followed, the primary goal of studying performance is to identify how morphological features interact with each other and the environment to affect fitness (45). This popular quantitative approach is a powerful tool for demonstrating natural selection in the field and for revealing patterns that suggest which morphological features might be adaptive in which ecological contexts.

IMPORTANCE OF MECHANISTIC INFORMATION The examples described above of the nonlinear ways in which morphology can affect performance illustrate that the "morphology⟶performance" connection can be complex and surprising. Nonetheless, many studies using the "morphology⟶performance⟶fitness" methodology have relied on statistical correlations between morphological features and performance or fitness but have not included mechanistic analyses of how the features cause the correlated effects (e.g. 11, 16, 44, 49, 61, 63, 70, 97, 98, 127, 142, 143, 198, 199, 228). Even the classic studies correlating garter snake performance with morphology (11, 97), morphology with fitness (9), and performance with fitness (98) have not been complemented by experimental studies investigating the mechanisms by which vertebral number or tail length produce differences in burst speed, or by which burst speed improves survivorship.

Because the morphology⟶performance⟶fitness methodology is descriptive rather than mechanistic, a major limitation of this approach, discussed by

Arnold (7) and others (e.g. 88, 96, 133, 134), is that unmeasured morphological variables (that correlate with those that are measured) may be responsible for the performance differences assessed, and that unmeasured aspects of performance (that correlate with those assessed) may be the actual focus of selection. In addition, we must remember the other warnings (listed in the Morphology as a Tool to Infer Function or Ecological Role section above) about misconceptions that can arise when mechanism-blind correlations are made between morphology and performance. Hence, one means by which organismal-level mechanistic studies can enhance research in evolutionary biology is by providing the information necessary to prevent such misinterpretations of correlational data.

ADAPTATION CANNOT BE INFERRED FROM EFFECTS OF MORPHOLOGY ON PERFORMANCE Both mechanistic and correlational studies that focus only on the relationship between structure and performance can be misleading when used to infer adaptation. An untested assumption underlying many such studies is that a performance advantage translates into increased fitness (discussed by 7, 15, 45). There are a number of limitations of performance testing that call this assumption into question:

1. The aspect of performance measured may not be important to the biology of the organism in nature (74, 135, 228), or may play a different role in the life of the organism than we assumed. For example, tall, slim benthic organisms made of stiff, brittle tissues are susceptible to breakage in waves (seemingly “poor” performance), but breakage can be an important mechanism of asexual reproduction and dispersal by corals with such morphologies, which can therefore thrive on wave-swept reef crests (reviewed in 113). Similarly, rapidly growing seaweeds with weak stipes and holdfasts (“poor” performance) may be as successful in habitats where they can reproduce before seasonal storms hit as are stronger kelp (“good” performance) that grow more slowly, but that survive the storms (115).

2. Most performance studies are done on adults, even though organisms change properties as they grow and environments vary with time (diurnally, seasonally, and from year to year). The examples of the size-dependent and context-dependent effects of morphology on performance cited above should make us realize the importance of assessing performance at different stages in an organism’s ontogeny. One way to deal with this problem is to devise performance measures, such as the environmental stress factor described in (102), that relate the performance of an organism at each stage of its ontogeny to the environmental conditions it encounters at that stage.

3. Lack of information on the genetic basis of the morphological or performance differences studied limits the evolutionary conclusions that can be drawn from such experiments (108).

4. Morphological features that improve performance do not necessarily arise via natural selection (discussed by e.g. 69, 83, 131). Some features may be epiphenomena of how a structure is produced (e.g. 68, 83), such as the ridges on clam shells that may improve burrowing (208), or the shapes of sea urchin skeletons that correlate with their water-flow habitats (13). Sometimes wear and tear in the environment can improve the performance of a structure. For example, pruning of kelp by limpet foraging can reduce their chances of being ripped away by storm waves (19), chipping of barnacle shells by wave-borne debris can produce more breakage-resistant shapes (186), wear of radular teeth in snails can sharpen their cutting edges (83), and passive orientation of gorgonian sea fans by hydrodynamic forces (231) can increase their suspension-feeding rates (139). Of course, the growth rules and breakage patterns described above could themselves be the result of natural selection.

Paleontologists: The Interpretation of Fossils

BACKGROUND The ways in which morphological data are used to infer the function of fossil organisms are reviewed by Hickman (83, 84), Lauder (133), and Van Valkenburgh (222). Perhaps the most commonly used approach is analogy with living species of similar morphology. Analogy arguments are most convincing if the living organisms that possess a particular structure all use it in the same way, and if the structure does not appear in the fossil record before its hypothesized function was possible (e.g. features for arboreality should not precede the origin of vascular plants—222). Homology among living species can also be used to infer the functions of extinct organisms: Ancestral character states of functions are determined by mapping functions of living organisms onto a phylogeny; then the functions of extinct taxa are inferred by their position within particular clades (75). Another approach to inferring the function of extinct organisms is the paradigm method in which morphological features are compared with theoretical optimal designs for particular functions. If a fossil structure is close to the ideal design for accomplishing some function, it is inferred that the fossil structure probably served that function (84, 133, 222, 229). This approach has limited usefulness since there are many reasons that a structure might not be optimal for a function that it serves (e.g. 42, 57, 58, 68, 72, 152, 177, 217, 232). Both the analogy and paradigm methods suffer from the problems (discussed above) of assuming that morphology is a reliable predictor of function, while the homology method is only as reliable as the phylogenetic hypothesis on which it is based.

USEFULNESS AND LIMITATIONS OF MECHANISTIC STUDIES One way to avoid these problems is to conduct performance tests using physical or mathematical models of fossil organisms (e.g. 105, 107, 133, 196). Obviously this approach is limited to testing hypotheses about physical functions. Furthermore, even if such biomechanical studies show that a fossil structure could have carried out some task or improved the performance of some function, that does not reveal the role that morphological feature served in the life of the organism; the best we can hope to accomplish with such quantitative studies is to reject functional hypotheses that are physically impossible (105–107, 133).

Several potential pitfalls of mechanistic analyses of fossil function are illustrated by the study of Marden & Kramer (149, 150), who presented an intriguing argument by analogy with living stoneflies that the protowings of early insects served in skimming or sailing locomotion on the surface of water. They showed by wing-trimming experiments that skimming and sailing performance are improved by increasing wing length. However, in interpreting these results they fell prey to a flaw in logic and they ignored available evidence on the phylogenetic relationships of the organisms involved. The flaw in logic was the assertion (148) that evidence supporting one functional hypothesis (surface skimming) implies rejection of alternate hypotheses (e.g. parachuting, gliding, thermoregulation), even though these alternative functions may not be mutually exclusive (107). The phylogenetic faux pas was the proposition that surface skimming represents an intermediate stage in the evolution of insect wings in Pterygotes, and this ancestral function has been retained by primitive stoneflies. This interpretation ignores the fact that stoneflies are members of the Neoptera, whose wing characteristics are considered to represent a derived condition (240). Without phylogenetic support, all the feasible scenarios proposed for the evolution of insect wings remain speculative (240).

Internalists: Study of the Origin of Evolutionary Novelty

The mechanisms by which novel phenotypes arise during evolution and the mechanisms responsible for the rapid morphological transformations that are recorded in the fossil record are challenging and contentious issues in evolutionary biology (history reviewed by 58, 65). Evidence emerging from mechanistic studies about the nonlinear size- and context-dependent effects of morphology on performance suggest another simple mechanism by which evolutionary novelty might arise.

BACKGROUND Evolutionary novelty or innovation has been defined in various ways (233): Some investigators require that it be a qualitative deviation in morphology (10, 160, 161), whereas others refer to a morphological, physiological, or behavioral change that permits the assumption of a new function (15, 94, 168). A key innovation is a novel feature that characterizes a clade and allows a subsequent diversification of the lineage (20, 134, 136, 140, 175, 202). The concept of key innovation has been criticized (e.g. 33, 94, 136) for a variety of reasons, including the difficulty of choosing which feature is the novelty and of demonstrating the causal link between that feature and a subsequent increased speciation rate. Nonetheless, various methodologies have been proposed to identify key innovations (e.g. 136, 212), and a number of examples of key innovations have been proposed (e.g. 134). A key adaptation is a novelty that reduces the costs of tradeoffs between various functions a species performs, thereby permitting that species to invade a niche when the incumbent species in that niche becomes extinct (201). A preadaptation is a feature that acquires a new biological role when organisms interact with their environment in a different way (e.g. 20, 57, 227). A preadaptation becomes an exaptation, a trait whose origins in a clade were due to selective pressures different from those that currently maintain it (69).

The idea of uncoupling (or decoupling) has provided a conceptual framework for much of the discussion of the origin of novelty (e.g. 10, 57, 128, 134, 202, 233). The basic argument is that coupling (e.g. one structure serving several functions, some function depending on several interrelated structures, or a change in one structure necessitating changes in others via pleiotropic effects or via their interconnection during morphogenesis) leads to evolutionary stasis because of the difficulty of changing one trait without negative effects on other features coupled to it (132). Examples of decoupling permitting evolutionary change (reviewed in 128, 202) include duplication of structural elements (if one set takes on a new function, the original function is not compromised), and loss of an old function (the structures that once performed it are free to be involved in new functions). However, some authors have argued that phenotypic plasticity permits suites of coupled characters to change in a coordinated way such that a complex organism's phenotype can shift rapidly with little genetic change (160, 238).

SOURCES OF NOVELTY: NEW BEHAVIORS AND CHANGES IN DEVELOPMENTAL PROGRAM

There are different views about the origin of novelty. While some investigators argue that behavioral shifts precede structural changes, others focus on the origins of new morphologies during development.

Behavioral shifts may precede morphological or physiological changes because behavior is more labile than morphology, and because natural selection should favor individuals showing compensatory behavior if the environment changes (e.g. 89, 161, 168, 227, 238; and others reviewed by 47, 72, 234).

Range expansion into a novel habitat can also provide a new set of selective forces on a population (examples discussed in 134). Furthermore, changes in the motor pattern controlling the kinematics of existing structures can produce novel functions (133). Once new behaviors or functions are acquired, selection should favor morphological variations that facilitate the new activity (161).

Small modifications in developmental program can lead to large changes in morphology (i.e. novelties) (e.g. 1, 23, 65, 94, 160, 161, 195). While the basic conceptual framework for this view has been formalized in terms of heterochrony (changes in the relative rates of different developmental processes) (e.g. 1), the nuts-and-bolts evidence for how changes in development can occur is coming from mechanistic studies, such as those of homeobox genes (reviewed by 65) and of the biomechanics of morphogenesis (reviewed by 38, 117).

MECHANISTIC STUDIES REVEAL ANOTHER POTENTIAL SOURCE OF NOVELTY New functions and novel consequences of changes in morphology can arise simply as the result of physics. As the examples described above illustrate, a simple change in environmental physical conditions or in body size can sometimes suffice to alter function. Although I think that both behavioral changes and alterations in developmental programs are important sources of novelty, it is possible for innovation to occur without either.

Mechanistic studies also illustrate that a common form of decoupling can be simply the lack of dependence of performance on morphology. Such permission for diversity of form without performance consequences may free structures to vary randomly or to respond to selection on other functions.

Although many ecomorphologists view size as a confounding factor in their analyses and propose various statistical techniques to eliminate size effects (e.g. 63, 228), I think it is important to consider size effects if one is addressing evolutionary questions. Most studies of size in biology have focused on the allometric changes required to maintain function as organisms grow or lineages evolve (e.g. 2, 27, 46, 102, 125, 126, 154, 167, 184, 205). If size changes over evolutionary time, such allometric growth of different parts of organisms might lead to new arrangements of these components and hence to innovations (e.g. 1, 136, 165). Of course, another way to think about allometry is to consider that if organisms do not change their form as they enlarge, their function does change, and such functional changes might be a source of evolutionary novelty.

There is ample evidence for selection on body size (reviewed by e.g. 24), and there are many examples in the fossil record of size changes within lineages over evolutionary time (reviewed by e.g. 93, 125, 126). The evolutionary trend in many, but certainly not all (93), lineages is that size increased with time (Cope's rule). This may be an artifact of better preservation and bias in observation of large organisms in the fossil record (125), or it may be that the founders of lineages tended to be small, and as size diversified, descendants on average got larger (93, 214). Fossil evidence indicates that many higher taxa arose from small ancestors (214). Stanley (214) suggested that small organisms were more likely to be founders of lineages than were large ones because little organisms are less subject to allometric constraints and therefore are more likely to give rise to novel types, while LaBarbera (126) pointed out that, even if the probability of breakthrough is the same at all body sizes, there are more small species.

The species diversity of small organisms is greater than that of large ones (e.g. 125, 163, 211), but the causes remain the subject of speculation (e.g. 33). One view is that there are fewer physical constraints on body form at small size (e.g. 21, 214). Another view is that ecosystems have more niches at small size (125) due to the fractal nature of habitats (159, 243).

The observations compiled above lead me to speculate about another potential mechanism to add to the list of ways of generating evolutionary innovation. Morphological and kinematic diversity may accumulate at small size without functional consequence, but such novelties may not assume new functional roles until there is a size increase and morphology matters. The structural diversity that did not affect performance at small size might gain functional significance at larger size; not only might features that were selectively neutral at small size become subject to selection at larger size, but novel functions might also become physically possible. Müller (160) has also suggested that evolutionary innovation should be associated with changes in size, basing his argument on evidence that size changes in developing embryos can affect pattern formation, thereby producing novelties in adult morphology.

If size changes tend to lead to evolutionary innovation, then I might speculate that the rate of evolutionary change would correlate with the rate of size change in a lineage. If we turn to the fossil record for evidence, and if we assume that short taxon longevity is a rough indication of rapid evolutionary change (i.e. high rates of modification or extinction), then the data from Hallam (76) for Jurassic ammonites and bivalves (replotted in Figure 7) is consistent with my speculation, but this obviously bears further investigation.

The Phylogenetic Approach and the Usefulness of Mechanistic Morphological Research

Modern studies of adaptation stress the importance of integrating analyses of structure, function, and fitness with phylogenetic history (16, 26, 45, 63, 68, 73, 80, 88, 89, 99, 129, 131, 136, 141, 144, 198, 222, 239). Unfortunately, enthusiasm for this approach has produced a climate in which mechanistic research can be dismissed when done without a phylogeny in hand. This dismissal ignores

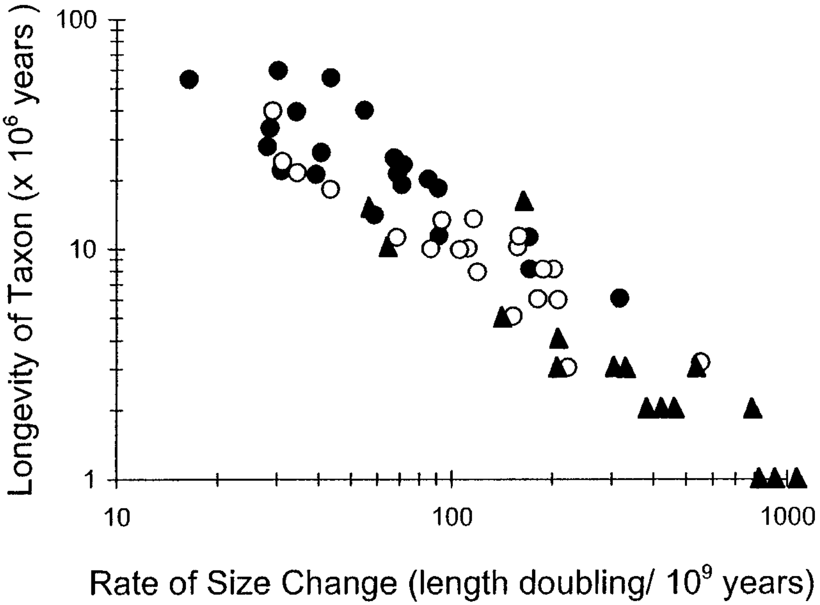

Figure 7 Longevity of each taxon in the fossil record, plotted as a function of the rate of change of body size, for Jurassic bivalved mollusks (*circles*) and ammonites (*triangles*). Solid symbols represent genera, and open symbols represent species. [Replotted using data digitized from Figure 1 of (76.)]

the fact many mechanistic studies do not have the identification of adaptations as their goal, but rather simply seek to unravel how (i.e. mechanism of operation), not why (i.e. evolutionary history) performance depends on morphology. I hope that the examples cited in this review will serve as a reminder that such mechanistic "how" information can also provide insights about evolutionary questions.

CONCLUSIONS

Quantitative mechanistic analyses of how function depends on biological form, and on the ecological context in which an organism operates, should complement descriptive statistical and phylogenetic studies to provide insights about ecological and evolutionary questions. Such quantitative studies have shown that the relationship between morphology and performance is often nonlinear and sometimes surprising. These mechanistic studies not only reveal potential misconceptions that can arise from the descriptive statistical analyses often used in ecological and evolutionary research, but they also show how new functions, and novel consequences of changes in morphology, can arise simply as the result of changes in size or habitat.

> "... You ask me whom the Macrocystis alga hugs in its arms?
> Study, study it, at a certain hour, in a certain sea I know.
> ... Or the crystal architecture of the sea anemone?
> ... I will tell you the ocean knows this, that life in its jewel boxes
> is endless as the sand,...
> ... I walked around as you do, investigating..."
>
> Pablo Neruda, *Enigmas* (164)

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