

Consequences of Size Change During Ontogeny and Evolution

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Changes in body size can occur during the lifetime of an individual organism as it grows, or can occur over many generations during the evolution of a lineage. Most studies of body size either explore how function is maintained at different sizes, or seek mechanistic explanations for the patterns we see in how features such as shape, metabolic rate, or life history vary with body size [7, 40, 52] (e.g., Brown this volume; Biewener this volume). My purpose here is to complement this literature about the consequences of *being* one size or another with an exploration of some of the functional consequences of *changing* size.

Function can shift as size changes, but the particular consequences of a size change can depend on factors such as the environment and morphology of the organism. This chapter focuses first on functional consequences of changing size, and then considers how the effects of morphological features on performance can be altered as size changes. This chapter concludes by considering how the consequences of a size change might be affected by: (1) the size range in which the change occurs, (2) the habitat, and (3) the structural design of the organism. I introduce each of these topics with a few examples, mostly biomechanical, and then discuss in more general terms their ecological or evolutionary consequences.

1 TRANSITIONS IN FUNCTION AS SIZE CHANGES

1.1 EXAMPLES OF FUNCTIONAL SHIFTS ACCOMPANYING SIZE CHANGE

1.1.1 Shifts in Hydrodynamic Function. Many important biological processes (such as respiration, and locomotion) depend on how organisms interact with the fluid medium, water or air, around them. The Reynolds number (\mathcal{R}) of a structure moving through a fluid represents the relative importance of inertial to viscous forces determining how the fluid moves ($\mathcal{R} = LU/\nu$, where L is a linear dimension of the structure, U is fluid velocity relative to it, and ν is kinematic viscosity of the fluid) [57]. At high \mathcal{R} 's (e.g., large, rapidly moving structures), inertial forces predominate and flow is messy and turbulent, whereas at low \mathcal{R} 's (e.g., small, slowly moving structures), viscosity damps out disturbances in the fluid and flow is smooth and orderly. Thus, we should expect changes in biological processes that involve fluids as body size (and hence \mathcal{R}) changes.

1.1.2 Hairy Little Legs. Many animals from different phyla use appendages bearing arrays of hairs (Figure 1(a)–(e)) to capture molecules from the surrounding fluid (e.g., feathery gills or olfactory antennae), to capture particles (e.g., hairy suspension-feeding appendages), or to move the fluid around them (e.g., setulose appendages used to fly, swim, or create ventilatory currents). When a particular type of structure is so ubiquitous among organisms and serves such critical biological functions, it is important to figure out how it works, and how its function is affected by its size.

The performance of all the functions mentioned above (e.g., capturing molecules or particles, moving water or air) depend on how the arrays of hairs interact with the fluid around them. Therefore, the first step in analyzing how these structures work is to figure out how fluid moves around and through them. The \mathcal{R} 's at which the hairs on the types of structures listed above operate [8, 9, 30, 35, 38, 51] (using hair diameter for L) range between 10–5 and 10. In this \mathcal{R} range viscosity is very important in determining flow patterns (although we cannot ignore the effects of inertia at the upper end of this \mathcal{R} range). 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 develops between the surface and the free-stream flow. The layer of fluid along a solid surface in which this velocity gradient exists is called the boundary layer. Similarly, when a structure moves through water or air, the fluid contacting its surface is carried along with it and a boundary layer of sheared fluid develops along the structure's surface. The lower the \mathcal{R} , the thicker this layer of sheared fluid can be relative to the dimensions of the structure. Thus, in the case of viscous flow around a hair, the layer of fluid moving along with the hair can be quite thick relative to the hair's diameter, and little fluid may move through the gaps between adjacent hairs in an array [8, 9, 30]. Furthermore,

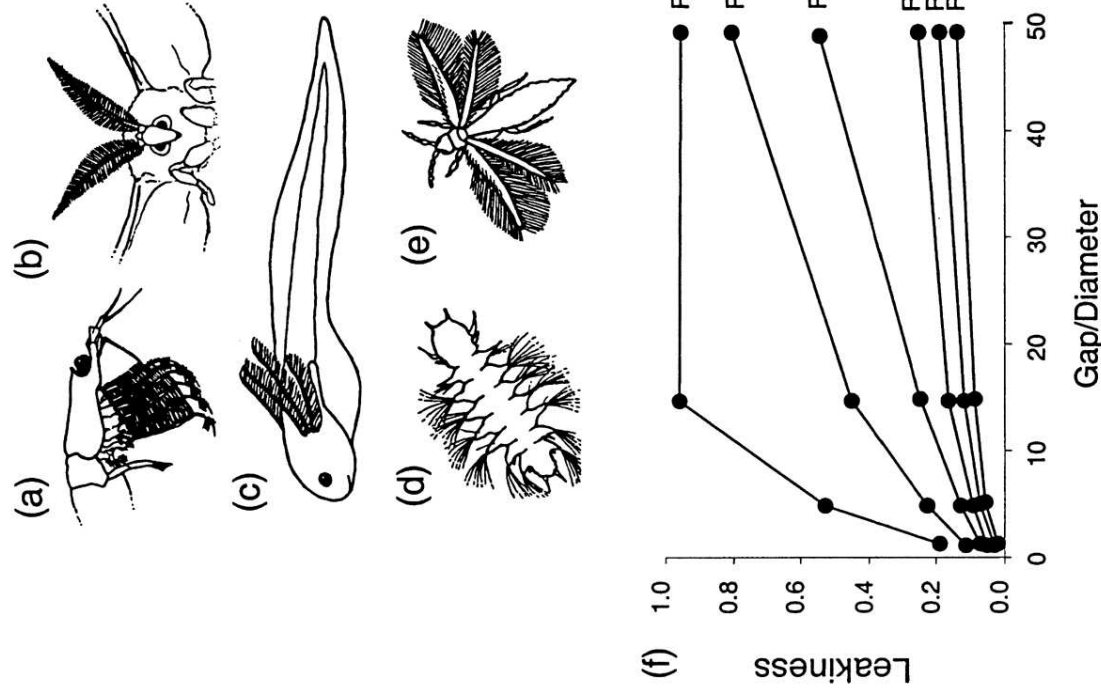


FIGURE 1 (a) Suspension-feeding appendages of a euphausiid ("krill"), Phylum Arthropoda. (b) Olfactory antennae of a male moth, Phylum Arthropoda. (c) External gills of a larval African lungfish, Phylum Chordata. (d) Swimming parapodia of a nereid larva, Phylum Annelida. (e) Wings of a thrips, Phylum Arthropoda. (f) Leakiness to fluid flow of the gap between neighboring hairs, plotted as a function of the ratio of the width of that gap to the diameter of a hair (redrawn from Koehl [32]). Each line represents a different Reynolds number.

flow is laminar (i.e., there is no turbulent mixing) in the \mathfrak{R} range in which these hairs operate; hence, the only way that molecules can be spread across streamlines is via molecular diffusion. Since humans operate at high \mathfrak{R} , we cannot trust our intuitions when considering the viscous flow around arrays of little hairs.

In order to understand how arrays of hairs capture molecules and particles, or push fluids around, the first thing that we need to figure out is whether fluid flows through the gaps between the hairs in an array, or flows around the array rather than through it. The leakiness (the proportion of the fluid encountering a gap between two hairs that flows through the gap rather than around the perimeter of the array of hairs [8]) of a hair-bearing structure determines, for example, whether or not the structure can function as a filter, the flux of molecules to hair surfaces, and the ability of the appendage to generate thrust or lift [30, 31]. Therefore, size (\mathfrak{R}) should affect all of these leakiness-dependent functions.

A general model of flow between neighboring hairs permits us to examine how the size, spacing, and speed of an array of hairs affects its leakiness (Figure 1(f)). Each line in Figure 1 represents a different \mathfrak{R} (i.e., a different size). At small hair sizes ($\mathfrak{R} = 10^{-5}$ to 10^{-3}), arrays of hairs have very low leakiness (i.e., only a small proportion of the water or air encountered actually goes through the gaps between hairs, while most flows around the array) and function like nonporous paddles. In contrast, from \mathfrak{R} 's of 10^{-2} to 1, a transition in leakiness occurs: a structure that functioned like a paddle at small size becomes a leaky sieve at larger size and filtering becomes possible. Thus, as hair-bearing appendages change size across this critical \mathfrak{R} range, their function switches.

A biological example of this transition in leakiness is provided by calanoid copepods, abundant planktonic crustaceans that play a critical link in many marine food webs between single-celled algae and higher trophic levels such as fish. Copepods capture single-celled algae using a pair of hairy feeding appendages, the second maxillae (M2's), which they fling apart from each other and then sweep back together [35]. Some species perform this capture motion with their setae (hairs) operating at \mathfrak{R} 's of order 10^{-2} ; their nonleaky, paddlelike M2's capture food by drawing a parcel of water containing an alga toward the mouth during the fling. In contrast, other species operate their M2's at setal \mathfrak{R} 's of one and filter their food from the water as they sweep toward each other. Thus, even though their M2 feeding motions look qualitatively similar, the physical mechanisms by which these two species of copepods capture food are different because they operate at \mathfrak{R} 's above and below the transition from paddle to sieve [30]. These results suggest that we might expect similar functional transitions during the ontogeny of the many aquatic larvae with setulose appendages that grow across this hair \mathfrak{R} range where the transition in leakiness occurs.

1.1.3 Swimming. Other examples of transition in hydrodynamic function as size (\mathfrak{R}) changes are provided by studies of the ontogeny of swimming. As brine shrimp larvae get bigger, their propulsive mechanism switches from drag-based rowing at low \mathfrak{R} to inertial swimming at higher \mathfrak{R} , even though the flapping motion of their appendages does not change [60, 61]. Similarly, larval fish switch from drag-based swimming at low \mathfrak{R} to inertial propulsion when they grow to higher \mathfrak{R} [4, 46]. Furthermore, as larval fish increase in size and the importance of viscous force declines at higher \mathfrak{R} , intermittent swimming becomes more energetically advantageous [59]. Scallops provide another example of transitions in swimming performance with changes in body size [11, 39]. Scallops 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, whereas larger scallops can jet; once $\mathfrak{R} > 3000$, scallops are big enough to use lift to get up off the substratum. However, when scallops grow even larger, they become poor swimmers again as their shells grow too heavy relative to the thrust they can generate.

1.1.4 Walking on Water. Whether or not animals can walk on water depends on their size. Some animals, such as water striders, are held up by the surface tension acting along the perimeters of their feet. Since the force holding the animal up is proportional to length, while the weight of the animal is proportional to volume, there is a body size above which animals cannot use the surface-tension mechanism to walk on water [1].

Some larger animals, such as basilisk lizards, can run on water using a different physical mechanism: the force to support the lizard's body 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 [17, 18]. There is also an upper limit to the body size for which this mechanism of locomotion on a water surface can work, since the weight that must be supported increases at a greater rate with body size than does the upward force that can be generated by the feet. These lizards also provide an example of another functional shift that can sometimes accompany increases in body size: at small size there can be permission for diversity in the ways in which the animals move their appendages without serious performance consequences, whereas at larger size limb movements can have a critical effect on performance [31]. Small basilisks, which have the capacity to generate a large force surplus relative to their body weight, can vary their limb movements considerably and still remain atop the water, whereas larger animals, which can generate barely enough force to support their weight, are constrained to a narrow range of leg and foot motions to run successfully on water [17, 18]. In the field, juveniles often run on water simply to move to another sunning spot, whereas adults venture onto the water only under duress.

1.1.5 Solar Panels and Wings. An example of how an isometric change in body size has the potential to generate novel function is provided by wind-tunnel experiments using models of fossil insects of a range of sizes [26, 27]. The physical models were used to test various hypotheses about the aerodynamic and thermoregulatory consequences of changes in the length of protowings on early insects. At small body size, short thoracic protowings improved thermoregulatory performance, but had negligible effect on aerodynamic gliding, parachuting, or turning performance; in contrast, protowings of the same relative length on larger models improved 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. (Of course, whether or not protowings served thermoregulatory or aerodynamic roles in early insects remains speculative, as do other feasible hypothesized functions, such as sexual signaling, gas exchange, or skimming along the surface of a body of water.)

1.1.6 Trophic Role. Examples of functional shifts that accompany size change can be found in ecological studies of the trophic roles played by certain species of animals as they grow. For instance, some benthic marine worms that feed on sediment particles as adults have juvenile stages that are herbivorous or carnivorous. This size-dependent switch in feeding mode is thought to occur because the guts of little juveniles are too small to permit adequate digestion of nutrient-poor sediment particles [22, 24, 50]. Similarly, the type of prey that can be caught and ingested by certain species of predators can shift as body size increases (e.g., snakes [19], fish [45]).

Some species of prey grow large enough to become invulnerable to particular species of predators. The classic example of this type of switch in function that occurs as organisms grow is the size refuge attained by large mussels, *Mytilus californianus*, from predation by starfish (*Pisaster ocraceus*) [48]. Since *Mytilus californianus* are important competitors for space on rocky shores along the Pacific coast of North America, their ability to undergo a transition from being the preferred prey of *Pisaster ocraceus* to being not eaten by this keystone predator can have profound effects on the structure of the communities of organisms in these habitats [48, 49].

1.2 WHERE TO EXPECT FUNCTIONAL SHIFTS TO OCCUR AS SIZE CHANGES

There are bound to be many yet to be studied examples of functional shifts that occur as size changes. Some hints of where to expect such changes in function can be gleaned from the dimensionless numbers, worked out by engineers, to describe the relative importance of different physical factors involved in a process. In some of the examples cited above, the relative importance of inertia to viscosity (\mathfrak{R}) depends on size (L). For biological functions involving momentum exchange between organisms and the water or air around them (e.g.,

swimming, flying, ventilation, circulation), we can expect to find functional shifts as \mathfrak{R} changes. Similarly, for biological functions involving transport of molecules, such as gas exchange, nutrient uptake, or smelling, the importance of fluid motion relative to molecular diffusion is given by the Péclet number ($\text{Pé} = LU/D$), where L is a linear dimension, U is velocity of the fluid relative to the structure, and D is the diffusion coefficient of the molecule of interest in the fluid) [57]. Like \mathfrak{R} , Pé depends on size (L). Pedestrian locomotion (walking, running) and swimming at the air-water interface depend on the importance of gravity relative to inertia (Froude number = U^2/gL), where g is the acceleration due to gravity), which also depends on size (L).

1.3 ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF FUNCTIONAL SHIFTS THAT OCCUR AS SIZE CHANGES

The examples cited above are but a few of the transitions infrequently that must accompany the size changes that occur during the ontogeny of an individual or the evolution of lineage. An important ecological consequence of such transitions is that a single species can play several different roles in a community if, for example, their feeding mode or their vulnerability to predation or physical disturbance changes as they grow [45, 48, 49]. An important evolutionary consequence of functional transitions that accompany size change is that new selective pressures on morphology can occur if a novel function is acquired as a lineage changes size over evolutionary time [26, 30].

2 TRANSITIONS IN THE EFFECTS OF MORPHOLOGY AND BEHAVIOR AS SIZE CHANGES

2.1 EXAMPLES OF SIZE-DEPENDENT CONSEQUENCES OF MORPHOLOGY AND BEHAVIOR

2.1.1 Hairy Little Legs. The hairy legs mentioned above provide examples of how the effects of a particular morphological characteristic or type of behavior can be altered as size changes. We have been using mathematical [8, 9, 30] and physical models [30, 38] to quantify how various structural or kinematic features of a row of hairs might affect its leakiness. For example, hair spacing has virtually no effect on leakiness at hair \mathfrak{R} 's of order 10^{-3} and lower, but as size increases to \mathfrak{R} 's of 10^{-2} to 1, spacing has an enormous effect on flow through the array of hairs. At even larger sizes ($\mathfrak{R} > 1$), hair spacing once again has no effect on leakiness (unless hairs are very close together) (Figure 1). Adding more hairs to a row of hairs reduces the leakiness of the array if $\mathfrak{R} < 1$, but has the opposite effect at larger size ($\mathfrak{R} > 1$). Similarly, as size changes, there are transitions in which behaviors can affect the leakiness of hairy appendages. For example, moving the appendage near a wall (such as the body surface) increases leakiness at \mathfrak{R} 's of 10^{-2} and lower, but not at

larger size. In contrast, speeding up appendage movement only affects leanness at \mathfrak{R} 's between 10^{-2} and one, but not at smaller or larger sizes. Thus, for hair-bearing appendages, a continuous change in size can lead to a discontinuous change in how particular morphological or behavioral traits affect performance.

2.1.2 Streamlining. The effect of body shape on drag depends on the size of the organism. Drag, a force which tends to push an organism in the direction that water or air flows past it, is due to skin friction (the resistance of the fluid in the boundary layer around the body to being sheared) at low \mathfrak{R} 's, but is due to skin friction plus form drag (the net pressure on a body behind which a wake has formed) at high \mathfrak{R} 's [57]. Streamlined body shapes (those with a long, tapered downstream end) reduce form drag compared with bluff body shapes of the same width because smaller wakes form behind the streamlined bodies, although the larger area of the long, tapered tail raises skin friction. Drag coefficient (C_D) is a dimensionless index of how drag-inducing a body shape is. For large organisms operating at high \mathfrak{R} 's, at which form drag is much greater than skin friction, streamlining reduces C_D , but for small organisms at low \mathfrak{R} that only experience skin friction, streamlining increases C_D . For example, C_D 's of globe ammonoid shells are higher than C_D 's of flat, streamlined shells at $\mathfrak{R} > 100$, but the reverse is true for smaller shells at lower \mathfrak{R} [23]. Similarly, the C_D of small ($\mathfrak{R} = 1$ to 10) benthic stream invertebrates is lower if their shape is more hemispherical, whereas the C_D of larger animals is lower ($\mathfrak{R} = 1000$) if they are more flattened [55].

2.1.3 Bumpy Skin. Body size determines whether or not bumps on the skin of an organism affect drag [6, 28, 56, 57]. When organisms are small, surface texture is buried in the boundary layer and has no effect on drag, whereas at very high \mathfrak{R} 's surface bumps can protrude through the boundary layer and increase skin friction drag. The net drag on streamlined bodies is simply increased by skin bumps once the critical \mathfrak{R} (i.e., size) is reached. Changes in body size have more complex consequences for organisms that are not streamlined: at small sizes (\mathfrak{R} 's) surface texture has no effect on drag, whereas at large sizes surface bumps increase the drag; however, at intermediate sizes surface bumps have the opposite effect and *decrease* the drag (mechanisms explained in Vogel [57] and Koehl [31]).

2.1.4 Gliding. The wing shape that improves the distance traveled by gliding animals or plant seeds depends on body size. Short, wide wings enhance gliding at small size, whereas long, narrow wings improve performance at large size [14].

2.2 ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF SIZE-DEPENDENT CONSEQUENCES OF MORPHOLOGY AND BEHAVIOR

The effects of structure or kinematics on performance can shift as size changes. Therefore, if size changes during the evolution of a lineage, then selection for different morphologies or behaviors can occur for the large species than can occur for the small ones, even if their function does not change. Ecomorphologists and paleontologists use morphological characters of organisms to infer their ecological roles, their function, or their performance of particular tasks relative to other organisms (reviewed in Koehl [31]). In doing so, they should be aware that a particular morphological trait may have very different effects on the performance of small organisms than it does on the functioning of larger ones. Which morphologies correlate with particular ecological roles can depend on size.

3 THE CONSEQUENCES OF SIZE CHANGES DEPEND ON SIZE

3.1 EXAMPLES OF SIZE-DEPENDENT EFFECTS OF SIZE CHANGE

In the introductory chapter of this book, Brown discusses examples of plotting power functions on both linear and logarithmic axes. If we look at linear plots of the performance of some process as a function of body size, it is easy to see that various aspects of performance vary with body size in nonlinear ways. The size ranges for which such nonlinear plots have steep slopes are the ranges in which a *change* in size can have important consequences. In contrast, within the size ranges for which the slope is very shallow, modifications of size make little difference to performance. If the sign of the slope of such a plot changes, then an increase in size can have the opposite effect for small organisms than for large ones.

3.1.1 Exponential Relationships Between Size and Performance. An example of an exponential curve is shown in Figure 2, a plot of predator handling time as a function of prey size [13]. 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.

Many aspects of mechanical performance also have exponential relationships to size. For example, the deflection of a bending beam bearing a distributed load is proportional to its L^4 , so the effect of a 10-cm increase in the height of a sessile, cantileverlike organism of a given width being bent by ambient water flow is small if the organism is short, but is large if an organism of the same width is tall [31]. There are many other examples of exponential relationships between function and size [1, 2, 40, 41, 57, 58], including the

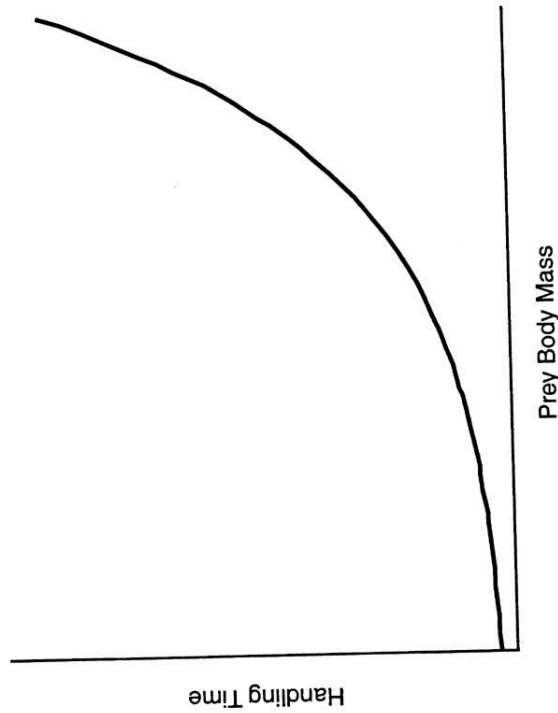


FIGURE 2 Handling time for a predator, plotted as a function of the body size of the prey (redrawn from a curve calculated by Emerson et al. [13]).

volume of fluid per time that can be pushed through a pipe (such as a blood vessel) by a given pressure difference, which is proportional to pipe diameter⁴ [4], or the weight that must be borne by a skeleton, which is proportional to body volume (proportional to L^3).

3.1.2 Optimal Sizes. If the plot of some aspect of an organism's performance as a function of body size goes through a maximum or a minimum, then the effect of increasing size reverses once it passes a critical value. One of many examples of how the consequence of a change in size can reverse as size increases is provided by Sebens [53], who analyzed the energetics of suspension-feeding animals. The energy available for growth and reproduction increases as such animals get larger up to a point, beyond which further increments in size have the opposite effect and reduce the excess energy for growth and gonad production (Figure 3). We usually consider such curves in the context of optimization analyses [3, 47], and we try to relate such maxima and minima to the peaks and troughs in adaptive landscapes [16, 25]. In addition, we might also consider that passing through such an inflection point represents the acquisition of a novel consequence for a size change.

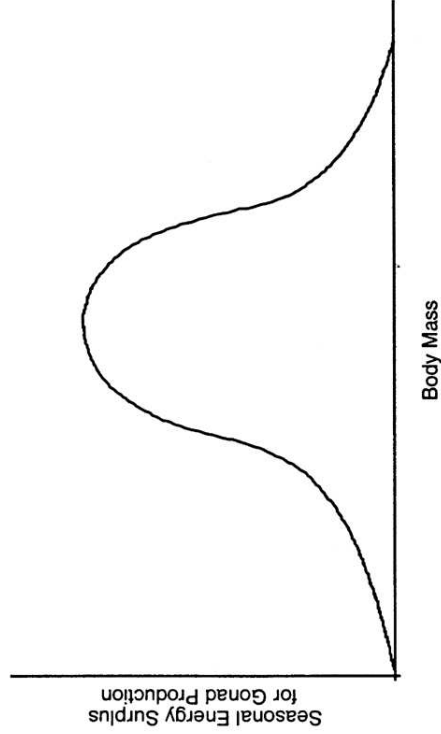


FIGURE 3 Energy surplus available for gonad production for an entire season, plotted as a function of the body mass of a passive suspension feeder, when prey sizes are normally distributed (redrawn from a curve calculated by Sebens [53]).

4 THE CONSEQUENCES OF SIZE CHANGE DEPEND ON MORPHOLOGY

4.1 EXAMPLES OF MORPHOLOGY-DEPENDENT EFFECTS OF SIZE CHANGE

4.1.1 Hairy Legs. Our recent work using dynamically scaled physical models to study the water flow through the setulose feeding appendages of copepods has shown that morphology affects the size at which the transition occurs between functioning like a nonleaky paddle and working like a leaky sieve. Coarsely meshed appendages become filters at smaller size than do appendages bearing closely spaced hairs [34].

4.1.2 Hydrodynamic Forces on Sessile Marine Organisms in Waves. The structure of the skeletal support tissues of sessile marine organisms can affect the hydrodynamic consequences of increasing size [31]. The microarchitecture of the support tissues determines their resistance to deformation, which in turn affects the flexural stiffness of the organism. Many marine organisms attached to the substratum, such as stony corals, are supported by stiff skeletal materials. In contrast, others like flexible gorgonians and seaweeds are made of tissues that are less stiff and can bend when subjected to hydrodynamic forces. All these attached organisms risk being dislodged or broken by ocean waves. We have been studying how the stiffness of their tissues affects the magnitude of the hydrodynamic forces they experience in the back-and-forth accelera-

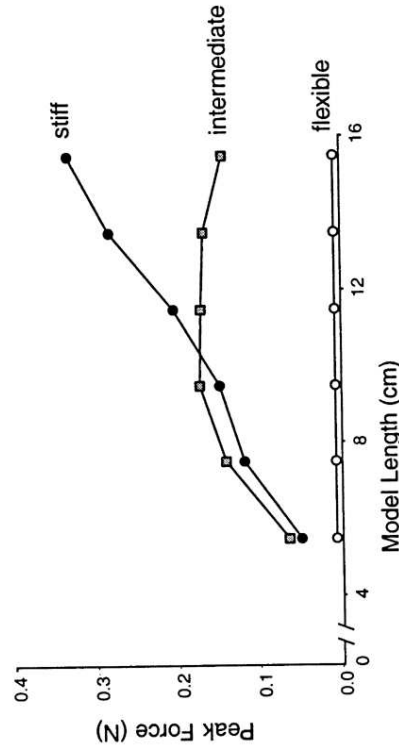


FIGURE 4 Peak hydrodynamic force in oscillatory flow measured on models of upright, planar benthic organisms, plotted as a function of model length. Each line represents a different flexural stiffness. (Redrawn from Koehl [31]).

tional flow they experience in waves. One approach that we have used is to build models of generic organisms, holding shape constant but using different materials to provide a range of flexural stiffness. We measured the hydrodynamic forces on such models of different lengths in a wave tank (Figure 4). As the stiff models "grew," the force increased. In contrast, the very flexible models flopped over into more streamlined shapes and went with the flow such that the force they bore did not measurably increase with length. A third type of size-dependent behavior was shown by the models of intermediate stiffness: lengthening increased hydrodynamic forces on short models, had no effect on models of intermediate length, and decreased forces on long models. Since deflection of a cantilever depends on L^4 , the longer the models of intermediate stiffness become, the more they bend over and go with the flow.

4.2 ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF MORPHOLOGY-DEPENDENT CONSEQUENCES OF SIZE CHANGE

If the effects of changing size depend on structure, then the consequences of growth or of evolutionary shifts in size can be different for organisms of various morphologies. Ecological modelers should be mindful that a single size-dependent expression may not describe the function of diverse members of a community. Furthermore, when organisms alter their morphology during ontogeny, the quantitative relationship between certain aspects of performance and body size can change. For example, when copepods shift from the body form of the nauplius larva to the morphology of the copepodid stages, the slope

of the log-log plot of mass-specific metabolic rate as a function of body mass switches from ~ 1 (indicating little change as size increases) to $\ll 1$ (indicating a decline as size increases) [15]. Thus, a single size-dependent expression may not even describe a single species in a community.

5 THE CONSEQUENCES OF SIZE CHANGE DEPEND ON HABITAT

5.1 EXAMPLES OF HABITAT-DEPENDENT EFFECTS OF SIZE CHANGE

5.1.1 Hydrodynamic Forces on Sessile Organisms. The effect of size on the hydrodynamic forces on stiff sessile organisms depends on whether they live in habitats exposed to waves or to unidirectional water currents [12]. When exposed to waves, organisms experience acceleration reaction force as well as drag. The acceleration reaction force is proportional to the volume of the organism, and hence increases with L^3 , while the attachment area of the organism is proportional to L^2 . Therefore, in wave-swept habitats an increase in body size leads to an increase in the probability of being swept off the shore by waves. In contrast, sessile organisms in habitats subjected to unidirectional water currents only experience drag force, which depends on their projected area. Since both drag and attachment strength are proportional to L^2 , growth does not impose an increased risk of being ripped off the substratum like it does in wave-swept habitats.

Water-flow habitat also affects the consequences of growth for flexible organisms, but differently from stiff organisms [31]. In unidirectional currents, both the drag and attachment strength of flexible creatures are proportional to L^2 , as for stiff organisms. However, flexible organisms in the back-and-forth flow of waves can experience a reduction in hydrodynamic forces as they increase in length beyond the distance the water travels before it stops and flows back the other way, as measured on real kelp in the field as well as on models in a wave tank [33].

5.1.2 Spawning by Sessile Organisms. Many attached marine organisms spawn gametes into the surrounding water. An increase in body height improves gamete transport and mixing in gentle currents, but has no effect in turbulent waves [31].

5.1.3 Suspension Feeding by Colonial Animals. The effect of an increase in the size of a colony of suspension-feeding bryozoans can depend on the hydrodynamic environment in which the colony lives [43, 44]. An increase in colony size can lead to a decrease in particle-capture rate per zooid in habitats characterized by slow currents, as upstream zooids deplete the water of food. However, in habitats exposed to rapidly flowing water, colony growth has the opposite effect on feeding rates per zooid: larger colonies are more effective than small

ones at slowing the water flowing through them enough that zooids can catch and hold on to food particles.

5.2 ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF HABITAT-DEPENDENT CONSEQUENCES OF SIZE CHANGE

Since the performance consequences of changing size can depend on habitat, analyses of size and scaling should be done in the context of the environment in which the organisms live. Furthermore, the habitat dependence of the effects of size suggests that, when organisms disperse to new habitats or when the environment changes, selection on body size can change. Striking examples of this are provided by the evolutionary size changes exhibited by isolated populations of mammals on islands where resource availability and predation pressure are different from those on the mainland (e.g., Lomolino [37]).

6 EVOLUTIONARY CONSEQUENCES OF SIZE CHANGES

6.1 ANOTHER POSSIBLE MECHANISM FOR THE ORIGIN OF NOVELTY

A variety of mechanisms have been proposed for the origin of novelty during the process of evolution (reviewed by Koehl [31]). Size change should be added to the list. There is ample evidence for selection on body size, and there are many examples in the fossil record of size changes within lineages over evolutionary time (reviewed by Koehl [31]). Many studies of organism size have explored how body allometry permits function to be maintained at different sizes. However, another way to think about allometry is to consider that if organisms do *not* change their form as they change in size, their function is altered, and such functional shifts might be a source of evolutionary innovation.

One obvious mechanism by which a change in body size might lead to evolutionary novelty is that a structure acquires a new function once size crosses some threshold. That structure then becomes subject to a different suite of selective pressures than it was when it performed the old function at the former size. A similar mechanism by which size change might contribute to evolutionary novelty is that morphological and kinematic diversity might accumulate at small size without consequences to the performance or fitness of the organisms, but might gain functional significance and thus become subject to natural selection at larger size (reviewed by Koehl [31]).

A third mechanism by which size change might lead to evolutionary innovation is that size differences in developing embryos can affect pattern formation, thereby producing novelties in adult morphology (reviewed by Koehl [31]).

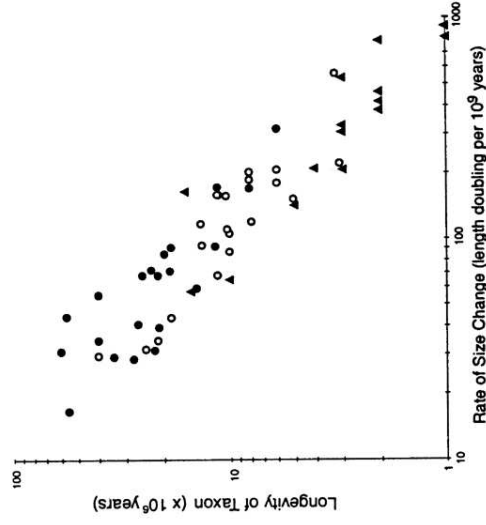


FIGURE 5 Longevity of each taxon in the fossil record, plotted as a function of the rate of change of body size, for Jurassic ammonites (each triangle represents a genus) and bivalved mollusks (each black circle represents a genus; each open circle represents a species). (Redrawn from Koehl [31]; data from Hallam [20].)

6.2 POSSIBLE EFFECTS OF SIZE CHANGE ON RATES OF EVOLUTION

Since shifts in size can be accompanied by alterations in function and changes in the consequences of particular morphological features, a reasonable speculation might be that rapid evolutionary change should tend to occur when size changes within a lineage. If we assume that short taxon longevity is a rough indication of rapid evolutionary change (i.e., high rates of modification or extinction), then Jurassic ammonites and bivalves (Figure 5) provide fossil evidence consistent with this speculation, but obviously this issue requires further study. For example, extinction might be due to acquisition of "poor" function accompanying a size change in the face of a shifting abiotic or biotic environment, or it might be the consequence of random events. Nonetheless, the pattern revealed by Hallam's data is intriguing.

7 CONCLUSIONS

Changes in body size can occur during the ontogeny of an individual or during the evolution of a lineage. The examples of the consequences of such size changes cited in this chapter illustrate that the effects of becoming larger or smaller are complicated, can involve dramatic transitions in function, and

can depend on the morphology and habitat of the organisms. My point in raising these examples is *not* that the consequences of changing size are too complex to be understood using simple rules. Quite to the contrary, my point is that basic physical principles permit us to understand and to predict such transitions in the functional consequences of size changes.

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