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MECHANICAL LIMITS TO SIZE IN WAVE-SWEPT ORGANISMS¹

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Abstract. Plants and animals that inhabit the intertidal zone of wave-swept shores are generally small relative to terrestrial or subtidal organisms. Various biological mechanisms have been proposed to account for this observation (competition, size-specific predation, food-limitation, etc.). However, these biological mechanisms are constrained to operate within the mechanical limitations imposed by the physical environment, and these limitations have never been thoroughly explored. We investigated the possibility that the observed limits to size in wave-swept organisms are due solely or in part to mechanical, rather than biological, factors.

The total force imposed on an organism by breaking waves and postbreaking flows is due to both the water's velocity and its acceleration. The force due to velocity (a combined effect of drag and lift) increases in strict proportion to the organism's structural strength as the organism increases in size, and therefore cannot act as a mechanical limit to size. In contrast, the force due to the water's acceleration increases faster than the organism's structural strength as the organism grows, and thus constitutes a potential mechanical limit to its size. We incorporated this fact into a model that predicts the probability that an organism will be destroyed (by breakage or dislodgement) as a function of five parameters that can be measured empirically: (1) the organism's size, (2) the organism's structural strength, (3) the maximum water acceleration in each wave, (4) the maximum water velocity at the time of maximum acceleration in each wave, and (5) the probability of encountering waves with given flow parameters.

The model was tested using a variety of organisms. For each, parameters 1–4 were measured or calculated; the probability of destruction, and the size-specific increment in this probability, were then predicted. For the limpets *Collisella pelta* and *Notoacmaea scutum*, the urchin *Strongylocentrotus purpuratus*, the mussel *Mytilus californianus* (when solitary), and the hydrocoral *Millepora complanata*, both the probability of destruction and the size-specific increase in the risk of destruction were determined to be substantial. It is conjectured that the size of individuals of these species may be limited as a result of mechanical factors, though the case of *M. complanata* is complicated by the possibility that breakage may act as a dispersal mechanism. In other cases (the snails *Thais canaliculata*, *T. emarginata*, and *Littorina scutulata*; the barnacle *Semibalanus cariosus*), the size-specific increment in the risk of destruction is small and the size limits imposed on these organisms are conjectured to be due to biological factors.

Our model also provides an approach to examining many potential effects of environmental stress caused by flowing water. For example, these methods may be applied to studies of: (1) life-history parameters (e.g., size at first reproduction, age at first reproduction, timing of reproductive cycles, length of possible reproductive lifetime), (2) the effects of gregarious settlement on the flow encountered, (3) the physical basis for patterns of disturbance, (4) the optimum (as opposed to the maximum) size of organisms, and (5) the energetic cost of maintaining a skeleton with an appropriate safety factor.

A definitive answer regarding the possibility of mechanical limits to size depends both upon an accurate measurement of the probability of encountering a wave of specific flow parameters and upon factors that are external to the model considered (e.g., life-history parameters). Further, due to their ability to move with the flow, organisms that are sufficiently flexible can escape the size limits imposed on more rigid organisms. Thus, some macroalgae attain large sizes (2–3 m in maximum dimension). The precise role of these factors awaits further research.

Key words: acceleration reaction; added mass; corals; disturbance; exposure; intertidal organisms; mechanical limits; size limits; size-specific mortality; wave forces.

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INTRODUCTION

Consequences of, and constraints on, the size of living things have long intrigued observers of nature (e.g., Galilei 1638, Thompson 1917, Haldane 1928). Not only do organisms of different size function (respire, capture food, grow, reproduce) at different rates (see

Schmidt-Nielsen 1974, McMahon 1975, 1980, Banse and Mosher 1980, Gray 1981, Platt and Silvert 1981, and references cited therein), but organisms of grossly different size often live in different physical realms (e.g., Haldane 1928, Went 1968, Horn et al. 1982). Furthermore, patterns exist in the ecological roles of organisms of different sizes (Hutchinson and MacArthur 1960, Van Valen 1973, Kerr 1974, Banse and Mosher 1980, Silvert and Platt 1981; but see Frost 1980) and in their size distribution through evolutionary time (e.g., Gould 1966, Bonner 1968, Stanley 1973). We report here the results of an examination of the mechanical factors that may define the upper boundary to size in organisms swept by ocean waves.

Upper limits to body size

Many factors may impose physical upper limits to body size. Since the volume of an organism is proportional to the cube of its length, whereas the surface area for exchange of materials as well as the cross-sectional area of skeletal elements (and hence their strength) are proportional to the square of length, many large organisms are shaped differently from comparable small ones in ways that permit area to keep pace with volume (Thompson 1917, Haldane 1928, Gould 1966, Stanley 1973, Schmidt-Nielsen 1974). Such allometric changes in morphology would eventually lead to structural absurdities (Gould 1966); if extremely large, skeletons would deflect too much, break, buckle, or be too bulky to be moved (Galilei 1638, Haldane 1928, Gould 1966, Currey 1970, McMahon 1973). In addition, the mechanical practicality or the metabolic cost of various types of locomotion (running, swimming, flying, burrowing) may set physical limits to body size (Gould 1966, Bonner 1968, Maynard-Smith 1968, Alexander 1971, Stanley 1973, Schmidt-Nielsen 1974; for more examples see Pedley 1977). Many other factors limiting the size of organisms have also been proposed.

Wave-swept shores are undoubtedly a physically harsh environment, and therefore ideal for examining the role played by the physical environment in limiting the size of, and, thereby, influencing the ecology of the associated organisms, those that inhabit the intertidal zone of rocky shores and coral reefs.

Wave-swept organisms are not large

One simple observation forms the basis for this study: benthic organisms that live near the water's surface on wave-swept shores do not attain large size. Not only are the largest of wave-swept organisms (seaweeds and corals, which rarely exceed 2–3 m in their greatest dimension) much smaller than the largest organisms on the face of the earth (whales, Sequoia trees; see Alexander 1971), but they are also smaller than the largest benthic marine organisms living in more protected habitats. This trend has been observed, for example,

on rocky temperate shores (Lewis 1968). Mussels and starfish are larger in those intertidal areas where there is less wave action, or subtidal areas where the water motion is less intense (Harger 1970, 1972, Paine 1976*a, b*). Many algae are stunted in conditions of high wave exposure (Schwenke 1971, Connell 1972), although there are exceptions on this trend (Schwenke 1971). Colonial animals such as gorgonians, hydroids, corals, and sponges produce taller colonies in deeper water where wave action is attenuated (Reidl 1971). Similar trends in maximum body size have been noted in tropical coral reef systems. On those reefs or portions of reefs most battered by waves, corals are smaller or have lower profiles than on more protected reef areas (Stoddart 1969, Glynn 1973, Endean 1976, Randall and Eldredge 1977, Smith and Harrison 1977, Adey 1978, Highsmith 1981). Within-species comparisons show the same trend for stony corals, gorgonians, and algae (Grassle 1973, Vosburgh 1977, 1982).

Why should wave-swept organisms be limited to these small sizes? Many biological factors may be responsible for the small sizes of these organisms (food limitation, size-specific predation, etc.), and these factors have been addressed by many of the studies of intertidal ecology cited above. However, biological interactions must operate within mechanical limits set by the physical environment. Such limits, which have never been defined for wave-swept organisms, may account for restrictions formerly attributed to biological factors. The hypothesis that there are purely mechanical limitations to the size to which organisms may grow in wave-swept environments is supported by considerable evidence, since large organisms are more likely than small ones to be ripped off hard substrata by waves (corals: Graus et al. 1977, Randall and Eldredge 1977, Adey 1978, Chamberlain 1978, Highsmith 1980, 1981, 1982; mussels: Harger 1970, Paine and Levin 1981; algae: Black 1976, Santelices et al. 1980; other rocky-shore organisms: see Connell 1972). Once this hypothesis has been further evaluated, the role played by biological interactions can be examined more objectively.

The role of accelerational flow

We base our argument on the consequences of unsteady, accelerational flow in wave-swept habitats. Most past studies on the forces exerted on wave-swept organisms have considered only the hydrodynamic forces due to steady, nonaccelerating water flow (Jones and Demetropoulos 1968, Branch and Marsh 1978; for exceptions see Carstens 1968, Koehl 1977*a*). This force is the drag force, F_d :

$$F_d \propto A_p \cdot U^2, \quad (1)$$

where A_p is the area of the organism exposed to flow, projected in the direction of flow, and U is water velocity (for explanations of all abbreviations, see Ap-

pendix 1). This force is applied to, and resisted by, some critical structure of the organism having an area A_c ; for example, the basal attachment area of an acorn barnacle. Thus the stress (force per unit area, σ) placed on the organism's structural material is:

$$\sigma = F_d/A_c \propto (A_p/A_c)U^2. \quad (2)$$

For an organism that maintains a fixed shape as it grows (i.e., one that grows isometrically) A_p/A_c is constant and

$$\sigma = B \cdot U^2, \quad (3)$$

where B is the appropriate constant of proportionality. It is evident from Eq. 3 that for steady flow the stress placed on an organism is independent of its size. Certainly, the larger the organism, the larger the force to which it is exposed; however, the area over which this force is applied is proportionally larger, so the stress is constant. Thus, the hydrodynamics of steady flow give no clue to size limitation in isometrically growing organisms as long as there is no significant spatial variation in U that would make bigger organisms encounter faster flow.

However, water flow in waves is not steady. Water alternately moves towards and away from shore and is thus periodically accelerated. When waves break, large accelerations accompany the turbulent eddies that are formed. Objects in accelerating flow experience a force, F_a , the acceleration reaction, in addition to the forces caused by the instantaneous water velocity. A more complete (though less than exhaustive) expression for the total force imposed on an organism is

$$F_{df} = (F_d + F_a) \propto (A_p \cdot U^2) + (V dU/dt), \quad (4)$$

where F_{df} is the total force in the direction of flow and V is the volume of water displaced by the organism (Batchelor 1967). We can obtain an expression for stress on the organism by dividing this equation by the critical area over which the force is applied, as follows. If we define a characteristic length $L = V/A_c$, then the stress on the organism is:

$$\sigma = F_{df}/A_c = B \cdot U^2 + B' \cdot L dU/dt, \quad (5)$$

where B and B' are the appropriate constants of proportionality. Thus, in an accelerating fluid the stress experienced by an organism is indeed a function of the organism's characteristic length: the larger the organism, the greater the stress. For any given accelerational flow, if L exceeds a certain value, σ exceeds the stress that the organism can sustain (the breaking stress), and the organism will dislodge or break. In this manner accelerating flow acts to set a potential mechanical limit to size.

In order to test this argument we: (1) created a model for the stresses placed on wave-swept organisms, (2) estimated the flow regime present on wave-swept shores, (3) measured the necessary hydrodynamic coefficients

and constants for particular wave-swept organisms, (4) measured the distribution of adhesive tenacity for various wave-swept species, and (5) applied the principles of the model to these species.

MATERIALS AND METHODS

We chose two ecosystems in which to test this theory of size limitation: (1) the exposed rocky shoreline of Washington and (2) a coral reef in the western Caribbean. The majority of the empirical measurements were carried out at various sites on Tatoosh Island, Washington, USA (48°23'N, 124°44'W). The principal site was a rock face inclined $\approx 35^\circ$ from horizontal and fully exposed to the prevailing southwesterly swells. The bottom slopes steeply down from the site, reaching a depth of 10 m (below mean lower low water) ≈ 30 m offshore. This depth is maintained for another 70 m out from the site before the bottom again slopes steeply downward. Depths of 80–100 m are reached within 1200 m of the site. Other measurements were conducted in various surge channels on Tatoosh. Further intertidal measurements were made at Muckaw Bay (≈ 3 km south of Tatoosh Island), and at Shi-Shi Beach (≈ 8 km south of Tatoosh Island), in both cases on rocks protected from the full force of the prevailing swells by the gently sloping bottom offshore. Measurements of wave height, coral morphology, and coral distribution were made at the Galeta Point Marine Laboratory of the Smithsonian Tropical Research Institute near Colon, Republic of Panama (9°34'N, 78°43'W). As with any intertidal site, the fine-scale topography of the sites used in this study is so complex that a detailed description would be of little use for fluid mechanical purposes.

Estimation of water velocity and acceleration

The water velocities and accelerations accompanying breaking waves were estimated from data collected at the exposed site on Tatoosh Island between December 1979 and November 1980. A wave-force telemetry system was placed in the rock surface as described by Denny (1982), and the magnitude and direction of hydrodynamic forces exerted on cast-plastic replicas of a limpet (*Collisella pelta*) and on spheres (1.9 cm diameter) were measured for each wave during the course of several tides. Approximately 3×10^4 force events were recorded. The data for this study were taken from the portion of the record that included the most violent waves (19–20 November 1980). During this period, swell heights at breaking were visually estimated to vary from 2 to 4 m. For each of 30 sequential large waves, the time vs. force record of the wave was used to calculate time vs. velocity and time vs. acceleration records by numerically solving the following rearrangement of Eq. 4:

$$dU/dt = (F_{df} - [\rho/2]C_d A_p U^2)/(\rho C_m V), \quad (6)$$

using a fourth-order Runge-Kutta method with the initial condition that $U = 0$ at $t = 0$. This choice of initial condition was arbitrary; however, after the first three iterations (i.e., about the first 2 ms of the time vs. force record) the results obtained are entirely insensitive to the choice. For the derivation of this equation see Eqs. 17–19 below. The volume, V , and projected area, A_p , of the limpet replica used in these measurements were determined; and the drag coefficient, C_d , and inertia coefficient, C_m , were empirically determined as described below. The density of seawater, ρ , was assumed to be constant, 1025 kg/m³.

Estimation of extreme wave conditions

The maximum size to which an organism can safely grow is in large part a function of the force caused by the most extreme wave that the organism can be expected to experience. Unfortunately, it is extremely difficult to measure accurately “the” extreme value for a randomly occurring phenomenon such as a breaking wave. For example, during this study low tides suitable for installing the telemetry system did not coincide with any severe storms, and the records obtained were therefore of waves of less than maximum size. Furthermore, it would have been hazardous and probably technically impossible to install the device during more extreme environmental conditions. The maximum values of velocity and acceleration, calculated as described above, were ≈ 14 m/s and ≈ 400 m/s². The maximum calculated acceleration occurred at a calculated velocity of 1.7 m/s, and thus, assuming that the water started with zero velocity, the force accelerating the water was applied for at most ≈ 4 ms. The response time of the transducer used was 8 ms (Denny 1982), so it is very likely that the transducer’s deflection lagged behind the force applied and that the forces measured are underestimates. Consequently the calculated velocities and accelerations are underestimates of the actual values for the relatively mild conditions encountered and thus may considerably underestimate the conditions accompanying storm waves. We used the calculated values as a rough guide to the lower limit of the actual maxima, and present data for velocities from 0 to 20 m/s and accelerations from 0 to 2000 m/s². Although we have no independent evidence to confirm this range of accelerations, there is confirmation for the range of velocities. From United States Navy (1973) records of deepwater waves off southwestern Vancouver Island, Canada (near the Tatoosh Island site), between 1949 and 1973 the maximum wave height was 7.75–9.75 m on 0.1% of the days when heights were recorded, and no waves higher than this were recorded. As shown in Eq. 14 below, the estimated maximum water velocity at the moment the wave breaks for a 9.75-m wave is ≈ 14 m/s, although this may increase as the wave crest plunges downwards (Carstens 1968). Further, the shoaling of waves as they near the shore may increase their height above that

observed in deep water. In light of these factors, the velocity range used here seems justified.

Measurement of drag and lift coefficients

Drag coefficients were measured for two standard shapes (sphere, hemisphere) and two species of locally abundant and characteristic shelled animals (an acorn barnacle, *Semibalanus cariosus*, and a limpet, *Collisella pelta*). Lift coefficients were measured for *S. cariosus* and *C. pelta*. The object to be tested was attached to the mounting bolt of a force transducer sensitive either to the force in the direction of water movement, F_{df} , or the force perpendicular to water movement, i.e., lift, F_l . The force transducer was mounted on the top wall of a recirculating water tank (similar to those described by Vogel and LaBarbera 1978), the mounting bolt extending through a hole in the wall so that the object was held within 1–2 mm of the wall. Each object was then subjected to steady water velocities up to ≈ 4 m/s. Under the assumption of fully turbulent flow, the boundary layer in the vicinity of the model was calculated to be < 5 mm (see Eq. 15 below). Mainstream velocities in the test section of the flow tank were measured with an electromagnetic flowmeter (Cushing Velometer 600P). The projected area of each object (in the direction of the force being measured) was determined by tracing an appropriately projected picture of the object onto a piece of paper, cutting out and weighing the paper within the traced area, and comparing its mass to that of a piece of paper of known area. For each object the force was measured at several water velocities and the lift and drag coefficients were calculated using the following equations (Vogel 1981):

$$C_d = 2F_d/(\rho A_p U^2) \quad (7)$$

$$C_l = 2F_l/(\rho A_p U^2) \quad (8)$$

In general, both C_d and C_l vary with object size, the physical characteristics of the fluid, and the fluid velocity. In order to compare coefficients between objects of different sizes, C_d and C_l were plotted as a function of Reynolds number, Re , a dimensionless measure of the relative contribution of inertial and viscous processes in determining flow patterns around objects:

$$Re = U \cdot L/\nu, \quad (9)$$

where U is the velocity of the fluid relative to the organism, L is a characteristic length of the organism, and ν is the fluid’s kinematic viscosity (1×10^{-6} m²/s) (Fig. 1). C_d values used in this study were obtained at $Re \approx 10^5$ (equivalent to a velocity of 10 m/s for an object 1 cm long), a value generally appropriate for the conditions encountered during breaking waves. A variety of water velocities and sizes of objects were considered in this study, corresponding to various Reynolds numbers higher and lower than the standard value used to estimate C_d and C_l . Thus, we may have slightly over- or underestimated the actual C_d and C_l values

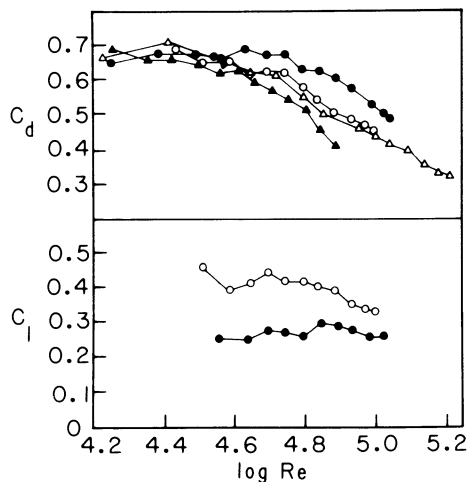


FIG. 1. Drag and lift coefficients (C_l and C_d) are plotted against the logarithm of Reynolds number (Re) for a variety of organisms and standard shapes: acorn barnacle, *Semibalanus cariosus* (●); limpet, *Colisella pelta* (○); hemisphere (△); sphere (▲). A lift force occurs only if hydrostatic pressure can be transmitted to the basal surface of the organism. Thus, an acorn barnacle glued to the rock with a solid adhesive (as in nature) would not experience a lift. The C_l values shown here were measured using a barnacle replica separated from the wall by a thin layer of water (an unnatural condition) and are presented solely to show that C_l for such shapes does not change substantially with Re .

in any given situation. The dependence of C_d and C_l on Re (and thereby on size) is likely to be most evident for simply shaped, smooth organisms such as the limpets we measured. As Vogel (1981) observes, the variation of C_d with Re decreases as the irregularity of the object increases; thus for a sea urchin, for example, C_d may vary little with Re . The C_d of plate-like organisms (such as the coral species discussed in Applications of the Model: Coral, below) varies only insignificantly (<5%) over the Re range 10^3 – 10^6 (Hoerner 1965). The effect of variations of C_d and C_l is examined more closely in the Discussion and in Appendix 2.

C_d and C_l were measured in steady flow. However, if the flow oscillates, C_d and C_l may vary as a function of another dimensionless parameter, the period parameter, K (Sarpkaya and Isaacson 1981):

$$K = U_m T / L, \tag{10}$$

where U_m is the maximum velocity, T is the period of oscillation, and L is a characteristic length (usually the organism's diameter). No attempt was made to measure changes in C_d and C_l as a function of K .

Drag and lift coefficients for objects for which empirical measurements were not made have been estimated using either the values presented by Hoerner (1965) or values equal to those found for similar-shaped objects. For example, values for the acorn barnacle *Balanus glandula* were assumed to be equal to those

for *S. cariosus*, for which measurements were obtained (Table 1).

Location of center of pressure

The lift imposed on an organism is the result of a pressure differential across the organism. This distributed lift force behaves as if the total lift were acting through a single point, the center of pressure. The center of pressure was determined as follows. Three hollow cones (basal diameter 11 cm; height/radius ratio = 0.5, 1.0, 2.0, respectively) were turned from acrylic plastic. In each, five ports (each ≈ 1 mm diameter) were drilled in a line running from the basal edge up to and including the apex (see Fig. 2). Each cone was attached to the top wall of the flow tank and exposed to a steady velocity of 0.63 m/s ($Re = 6.9 \times 10^4$). The base of the cone was not sealed to the wall, allowing hydrostatic pressure to be transmitted to the fluid beneath the cone. The hollow interior of the cone was loosely packed with glass wool to inhibit gross flow. The pressure difference between each port and a reference port located beneath the cone was measured manometrically using CCl_4 ($\rho_m = 1594 \text{ kg/m}^3$) as the manometer fluid. Readings were taken with the row of ports at angles to the water flow every 30° between 0° and 180° (0° = directly into the flow). Pressure readings were then summed to estimate the location of the center of pressure, C_p :

$$C_p = \frac{\sum_{\alpha=0^\circ}^{180^\circ} \sum_{i=0}^{N-1} \left(\frac{r_i + r_{i+1}}{2} \right)^2 (r_{i+1} - r_i) \rho_m g \left(\frac{\Delta H_i + \Delta H_{i+1}}{2} \right) \cos \alpha \cos \phi \Delta \alpha}{\sum_{\alpha=0^\circ}^{180^\circ} \sum_{i=0}^{N-1} \left(\frac{r_i + r_{i+1}}{2} \right) (r_{i+1} - r_i) \rho_m g \left(\frac{\Delta H_i + \Delta H_{i+1}}{2} \right) \cos \phi \Delta \alpha} \tag{11}$$

The definition of terms is shown in Fig. 2, and g is the acceleration due to gravity (9.8 m/s^2).

The center of pressure was found to lie along the midline and downstream of the apex by distances varying between $0.11 L_r$ (for the cone with height/radius = 2.0) and $0.29 L_r$ (for the cone with height/radius ratio = 0.5), where L_r is the cone radius. The average location of the center of pressure was $0.24 L_r$ downstream of the apex, and this value was used in subsequent calculations.

Measurement of added mass coefficient

The relationship between water acceleration and the force encountered by an organism depends in part on the shape of the organism. This effect of shape was accounted for by use of an added mass coefficient, C_a . This coefficient was determined as follows. Negative molds were prepared by embedding shells of *S. cariosus*, *C. pelta*, and *T. emarginata* in silicone sealant. Following removal of the shells, the molds were injected with urethane foam (Insta-Foam Products, Incorporated) to provide rigid, light replicas. These were coated with spray paint to prevent waterlogging, and the mass of each was measured on an electric balance to within 0.001 g. The mass of water displaced by each

TABLE 1. Adhesive tenacity values and hydrodynamic parameters for a variety of wave-swept organisms.

Species*	Shear strength (10 ⁵ N/m ²)		Tensile strength (10 ⁵ N/m ²)		Coefficients		
	$\bar{x} \pm SD$	No. samples	$\bar{x} \pm SD$	No. samples	Drag (C _d)	Lift (C _l)	Added mass (C _a)
Limpets							
<i>Colisella digitalis</i> (s)	3.85 ± 1.75	21			0.52	0.25	0.84
<i>Colisella digitalis</i> (m)	1.29 ± 0.91	21			0.52	0.25	0.84
<i>Colisella pelta</i> (s)			2.05 ± 0.93	30	0.45	0.47	0.68
<i>Colisella pelta</i> (m)			0.69 ± 0.48	30	0.45	0.47	0.68
<i>Notoacmaea scutum</i> (s)			1.73 ± 0.79	30	0.45	0.47	0.68
<i>Notoacmaea scutum</i> (m)			0.58 ± 0.41	30	0.45	0.47	0.68
<i>Patella vulgata</i> † (s)			1.86 ± 0.52				
<i>Patella vulgata</i> † (m)			0.62 ± 0.44				
<i>Patella cochlear</i> ‡ (s)			5.18 ± 0.94				
<i>Patella cochlear</i> ‡ (m)			1.73 ± 1.22				
<i>Patella argenvillei</i> ‡ (s)			4.67 ± 0.80				
<i>Patella argenvillei</i> ‡ (m)			1.56 ± 1.10				
<i>Patella longicosta</i> ‡ (s)			4.40 ± 1.15				
<i>Patella longicosta</i> ‡ (m)			1.47 ± 1.04				
<i>Patella granularis</i> ‡ (s)			3.25 ± 0.83				
<i>Patella granularis</i> ‡ (m)			1.07 ± 0.77				
<i>Patella granatina</i> ‡ (s)			2.71 ± 0.84				
<i>Patella granatina</i> ‡ (m)			0.91 ± 0.64				
<i>Patella oculus</i> ‡ (s)			1.95 ± 0.45				
<i>Patella oculus</i> ‡ (m)			0.65 ± 0.46				
Barnacles							
<i>Semibalanus cariosus</i>	3.29 ± 1.70	68			0.52		0.31
<i>Balanus glandula</i>	4.17 ± 2.31	49			0.52		0.73
<i>Balanus nubilis</i>	3.41 ± 1.13	10			0.52		0.31
<i>Balanus balanoides</i> §	9.25 ± 4.92						
Mussel							
<i>Mytilus californianus</i>							
End on	1.25 ± 0.40	50			0.20		0.20
Broadside	1.25 ± 0.40	50			0.80		1.00
Snails							
<i>Thais canaliculata</i> ¶ (s)	0.178# ± 0.034				0.67**		0.72
<i>Thais canaliculata</i> ¶ (m)	0.023 ± 0.009				0.67		0.72
<i>Thais emarginata</i> ¶ (s)	0.213 ± 0.134				0.67		0.72
<i>Thais emarginata</i> ¶ (m)	0.053 ± 0.035				0.67		0.72
<i>Littorina scutulata</i> ¶ (s)	0.310 ± 0.080				0.67		0.72
<i>Littorina scutulata</i> ¶ (m)	0.114 ± 0.022				0.67		0.72
Urchin							
<i>Strongylocentrotus purpuratus</i>	0.38 ± 0.23	30			1.00	0.55	0.38
Hydrocoral							
<i>Millepora complanata</i>			123 ± 43	39	1.80		5.00

* s: tenacity measured while the animal was stationary; m: tenacity measured while the animal was moving; moving values were calculated as described in Materials and Methods: Tenacity and Breaking Strength, except those for snails.

† Grenon and Walker 1982.

‡ Branch and Marsh 1978.

§ Yule and Walker 1984.

|| Equivalent stress values (see Applications of the Model: Mussels).

¶ Miller 1974.

Values for shear calculated as the same proportion of normal tenacity shown by *T. emarginata* (Miller 1974).

** A. R. Palmer, *personal communication*.

replica when immersed was determined to within 0.05 g by measuring the buoyant force it exerted.

Each replica was attached to the tip of a thin aluminum rod that was mounted on a force platform similar to that of Denny (1982). Acceleration of the replica was accomplished by suspending the force platform from the ceiling with wires ≈ 5 m long and allowing

the platform to swing like a pendulum. The replica and rod were at all times immersed in a long trough of water. Acceleration was measured using an accelerometer (Entran Devices type EGA-125) mounted on the tip of the rod next to the replica. Outputs of the accelerometer and force platform were monitored by a dual-channel strip chart recorder (Gould 2200). The

net force on the rod was measured independently and subtracted from measured forces for accelerated replicas. Since these intertidal animals normally are attached to the substratum, we chose to accelerate each replica parallel to a solid surface 1–2 mm from its base.

Since the velocity of the replica was low during the initial stages of acceleration (<0.1 s after starting from rest) the drag on the body was negligible and the total force was dominated by the inertia of the body and its acceleration reaction. Hence, the total force acting on the replica can be expressed in a form similar to Eq. 4:

$$F_{df} = [\rho C_a V dU/dt] + m dU/dt, \quad (12)$$

where F_{df} is the total force, C_a is the added mass coefficient, V is the volume of fluid displaced by the replica, m is the mass of the replica, and dU/dt is the acceleration. With measured or assumed values for F_{df} , ρ , m , V , and dU/dt , the added mass coefficient was determined from Eq. 12.

An inertia coefficient for stationary organisms in accelerating flows was defined as $C_m = 1 + C_a$, to include the effects of virtual buoyancy (Batchelor 1967: 409); values for C_a are shown in Table 1.

Tenacity and breaking strength

The adhesive tenacity, σ_{max} , expressed as the force per unit area required to dislodge the organism, was measured for eight species of intertidal animals on the Washington coast. Measurements for six of these species (*Collisella digitalis*, *Balanus glandula*, *Semibalanus cariosus*, *B. nubilus*, *Mytilus californianus*, and *Strongylocentrotus purpuratus*) were made on the exposed coast at Tatoosh Island or Shi-Shi Beach, and for the others (*C. pelta* and *Notoacmaea scutum*) at the Friday Harbor Marine Laboratory in Puget Sound. All animals tested were solitary: fully exposed to the prevailing flow and not shielded by any neighbors. The open coast measurements were conducted as follows. A loop of string was placed around the organism near its base, or, for mussels, where the byssus entered the shell, and the string was pulled parallel to the substratum until the animal was dislodged. This technique is appropriate for organisms with a shape or structures that prevent the string loop from slipping off when force is applied (e.g., the overhanging apex of the shell of *C. digitalis*). The force of dislodgment was measured with a recording spring scale of a design similar in principle to that of Jones and Demetropoulos (1968). The basal area of each organism, with the exception of *M. californianus* (see below), was estimated as the product of length and width. The recorded force was divided by this estimated area and multiplied by 1.42 to give a value for breaking strength in shear, $\sigma_{s,max}$, for each organism. Multiplication by the factor 1.42 was necessary because the shear stress varies across the base of an organism when loaded, as described above, reaching a maximum value at the center of the base. The maximum stress, that at which the material would

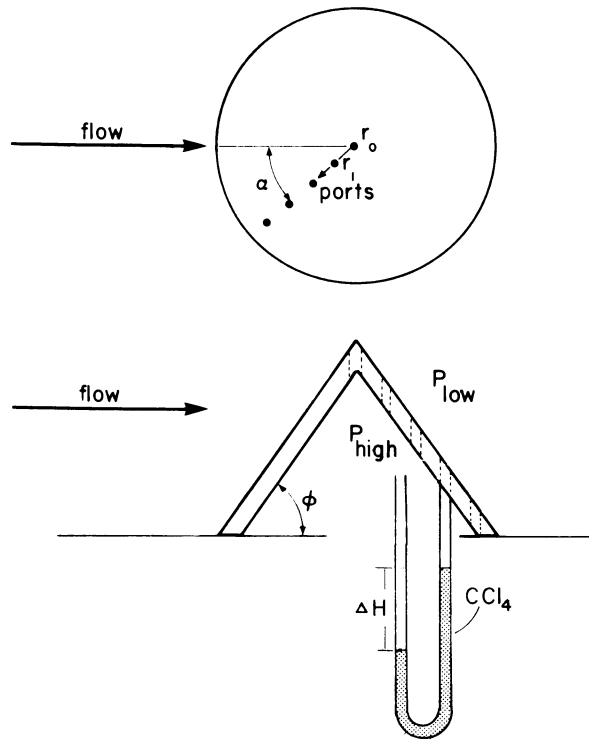


FIG. 2. A schematic diagram of the experimental method for determining the location of the center of pressure. A plastic cone is immersed in flowing water. The row of N ports is placed at some angle, α , relative to the direction of flow; r_1 is the distance from the apical port (r_0) to the first port. A manometer is used to measure the difference in pressure (ΔH) between each port and the underside of the cone.

break, is 1.33 times the average stress (force/basal area) if the base is circular, and 1.50 times the average stress if the base is rectangular (Timoshenko and Gere 1972). Since our animals had bases generally intermediate between these two shapes, an average value of 1.42 was chosen.

The two remaining limpet species, with shapes that were less accommodating, required a different technique. Measurements on *C. pelta* and *N. scutum* at Friday Harbor were made using a strain gauge transducer similar to that described by Denny (1982). A short piece of wire bent into a hook was attached to the shell apex with quick-setting epoxy glue. The force transducer was then attached to the hook, and force was applied perpendicular to the substratum until the animal was dislodged. The force of dislodgement was divided by foot area to give a value for the breaking strength in tension, $\sigma_{n,max}$.

All animals, whether on the open coast or at Friday Harbor, were tested while attached to the natural substratum, and each was lightly tapped or otherwise disturbed immediately before testing to induce it to adhere as tightly as it could.

Observed tenacity measures from this study and from

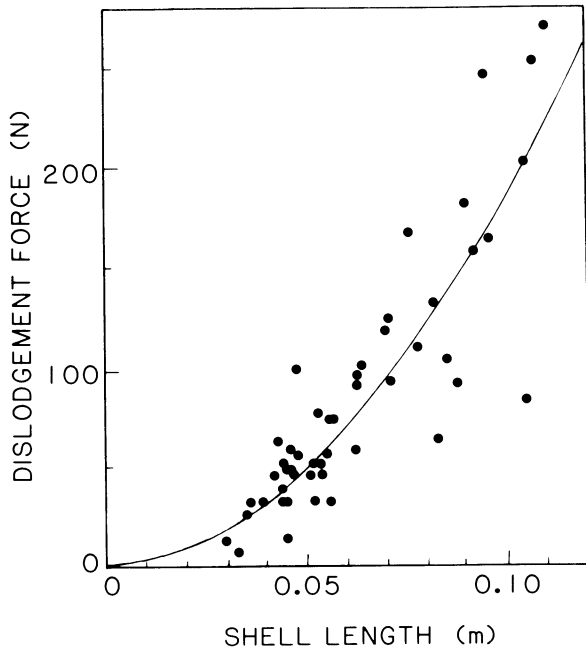


FIG. 3. Adhesive tenacity plotted against shell length for the mussel *Mytilus californianus*. The equation that describes these data is: $\text{Force} = 1.65 \times 10^4 L^{1.95}$, where Force is expressed in newtons and L in metres ($r = 0.86$).

the literature are summarized in Table 1. With the exception of the study of Miller (1974), all limpet tenacity values were determined for stationary animals. Unfortunately, Miller's values for the tenacity of moving limpets may not be correct since the values reported for stationary limpets, obtained under similar laboratory conditions (i.e., animals adhering to acrylic plastic) are substantially lower than those of other authors determined in the field. However, assuming that Miller's (1974) values for the ratio of moving to stationary tenacity are accurate, we have obtained estimates of the tenacity of moving limpets by multiplying the field-determined stationary tenacity value for each species by 0.334, the average ratio of moving to stationary tenacity for all species whose locomotion uses ditaxic waves, as determined by Miller.

The breaking strength of the hydrocoral *Millepora complanata* was determined by three-point bending tests. Fresh corals were collected from depths of < 1 m either at Galeta Point, or from the algal ridge off of the Limon island group, San Blas Islands, Republic of Panama. The corals were cut into strips ≈ 1 cm wide using a diamond saw; strips were cut parallel to the long axis of each coral blade (perpendicular to the substratum). For each test, the sample was supported near its ends and the distance between supports, D , was measured; by adding water to a bucket suspended by a wire from the centerline of the sample, the force acting on the sample was increased until the sample broke. The cross-sectional dimensions of the sample were measured at

the point of failure and the modulus of rupture (a measure of strength in bending) calculated according to Wainwright et al. (1976):

$$\text{modulus of rupture} = DFy/4I, \quad (13)$$

where F is the mass of bucket and water multiplied by the acceleration due to gravity, y is one-half the thickness of the sample, and I is the second moment of area of the cross section ($= \frac{1}{12}$ width of sample $\cdot y^3$ for a rectangular cross section). The modulus of rupture for the 39 samples tested was $12.3 \pm 1.47 \times 10^6$ N/m² (mean and 95% confidence interval).

Size and tenacity of mussels

Mussels were collected for morphological measurements from a 0.25×0.25 m quadrat haphazardly thrown onto the mussel bed at Tatoosh Island. The length of each of these mussels was measured to the nearest 0.2 mm with vernier calipers, and its volume was measured to the nearest 0.1 mL by immersion in a graduated cylinder containing water.

The force of dislodgement was measured for 50 mussels of various sizes pulled off the exposed rock surface at Tatoosh Island. A plot of dislodgement force vs. length of the mussel (Fig. 3) shows that the adhesive tenacity increases in proportion to $L^{1.95}$. A length vs. volume calculation for 182 mussels from Tatoosh shows that volume increases as $L^{2.86}$ (with volume expressed in cubic metres and L in metres, $\text{volume} = 0.06 L^{2.86}$; $r = 0.98$). Assuming that projected area is proportional to the $\frac{2}{3}$ power of volume, area increases as $L^{1.91}$. Thus, at least to the accuracy of this estimate, adhesive tenacity increases at the same rate as the projected area; this is one of the assumptions of analysis discussed below in Development of the Model.

If a mussel is treated as a streamlined body with a thickness approximately half its length, its C_d is ≈ 0.2 when it is end on to the flow and 0.8 when broadside, at the Re expected during wave flows (Hoerner 1965); we have used these values. C_m is ≈ 2.0 when the animal is oriented broadside to the flow and 1.2 when end on (Daniel 1982). The end-on, minimum value of projected area, $A_{p,min}$, was used to calculate an "equivalent stress" (force of dislodgement/ $A_{p,min}$) (Table 1).

WATER FLOW IN WAVE-SWEPT HABITATS

As background for a discussion of size limitation in wave-swept organisms, it is useful to examine in general terms the nature of the velocities and accelerations caused by waves and thus to illustrate the kinds of flows to which our analyses do (and do not) apply.

Intertidal organisms are exposed to breaking waves and postbreaking flows. The precise water movements occurring during the breaking of a wave are exceedingly complex, and mathematical analyses are only in the early stages of development (Cokelet 1977, 1979, Longuet-Higgins 1982, Peregrine 1983, Stive, *in press*). It is possible, however, to draw a general, approximate

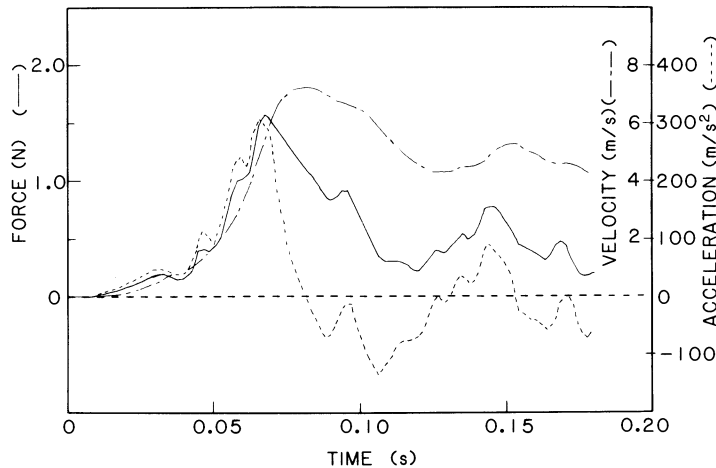


FIG. 4. Water velocity (---) and acceleration (---) during the initial portion of a typical wave, as well as the hydrodynamic force (—) they impose on an acorn barnacle, plotted against time.

picture of these flows. A wave approaching shore breaks when the height of the wave is approximately equal to the depth of the water (Galvin 1972). The wave can break in a number of ways, depending, in part, on the slope of the bottom leading to the shore. Where there are gradually sloping bottoms, waves curl over and the crest plunges forward at breaking; these conditions apply to the reef at Galeta Point. The bottom off Tatoosh Island, where much of this study was conducted, slopes steeply down to deep water and, consequently, the waves were generally intermediate between the types termed "surging" and "collapsing" by Galvin (1972). For this sort of breaking, the wave crest spills down the front of the wave body rather than arching over ahead of the body of the wave. For either case, at the moment of breaking the wave crest has velocity U , parallel to the bottom, given as a first approximation by linear wave theory as:

$$U = [g(H + Z)]^{1/2}, \quad (14)$$

where H and Z are the wave height and water depth, respectively (Wiegel 1964). Thus, for a 5-m wave breaking in water 5 m deep, the crest velocity is ≈ 10 m/s. In areas such as Tatoosh Island where the bottom slopes steeply away from the shore, waves often break very near or directly onto the emerged rocks of the shore. In such a case, water moving with a high velocity toward the rock is deflected by the impermeable surface, and, except for the area immediately under the wave where a plunging crest might first hit, the primary flow is a surge up the rock face (a turbulent bore, or subsequent run-up) at a velocity initially roughly equal to that of the crest velocity as calculated above (Carstens 1968, Peregrine 1972). Water velocity in post-breaking flows may increase somewhat as a turbulent bore collapses at the shoreline (Keller et al. 1960).

We envision three different flow regimes to which intertidal organisms may be exposed. They may ex-

perience (1) periodic flows *under* shallow-water waves, (2) a jet of water normal to the rock wall in the immediate area of a plunging crest, and/or (3) an impulsive onrush of a turbulent bore moving parallel to the surface of the rock wall. Carstens (1968) described the flow forces associated with the first two cases. He found that under shallow-water waves, accelerations are relatively small, on the order of 1 m/s^2 , and that flow forces depend largely on the fluid velocity. It is important to note, however, that this estimate of acceleration applies only to flows under nonbreaking waves and should not be used as an estimate of fluid accelerations once a wave has broken and run shoreward. Carstens (1968) also discusses the pressures associated with the impingement of a jet on an impermeable surface. These impact pressures may be quite large, with values exceeding $1.5 \times 10^7 \text{ N/m}^2$. Organisms exposed to such pressures may fail by implosive rupture rather than being sheared off the rock wall. The magnitude of impact pressure is a function of the acoustic velocity of water, which, in turn, depends quite strongly on the fractional volume of entrained air. With 10% air by volume, the acoustic velocity decays to about 10% of the value with no entrained air (Carstens 1968). Since Longuet-Higgins and Turner (1974) estimate an air content of $\approx 10\%$ for spilling breaking waves, impact pressures may be nearly an order of magnitude lower than those reported by Carstens (1968). Our records of wave force show that maximum force is generally reached 50–100 ms after initial contact with the water. These forces are clearly not due to impact pressures.

The third flow regime (a turbulent bore) is likely to be that most often encountered in the wave-swept environment and is the principal topic of this paper. When an unsubmerged organism encounters the onrush of a water front moving parallel to the surface, fluid accelerations can be quite large (Fig. 4). Because the flow is not directed into the substratum, there will be no sub-

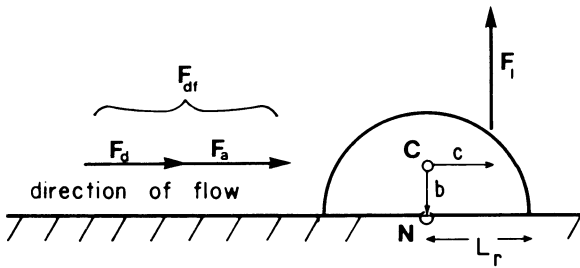


FIG. 5. A model of the hydrodynamic forces imposed on a hemisphere attached to a planar surface. The total force in the direction of flow, F_{df} , places a shear force (F_{df}) and a moment ($M_1 = F_{df} b$) on the hemisphere. The lift force, F_l , imposes a moment ($M_2 = F_{df} c$) on the hemisphere. C is the centroid and N is the location of the neutral axis (a line perpendicular to the plane of the drawing). L_r is the radius of the hemisphere. The components of F_{df} are drag, F_d , and the acceleration reaction, F_a .

stantial impact pressure, and the flow is likely to be quite turbulent. Local surface topography, water turbulence, and the formation along the substratum of a layer of fluid whose motion is retarded (the boundary layer) all have significant effects on the flow field encountered by an organism. In order to explore the magnitude of the forces associated with this flow we have made one crucial assumption: fluid speed and acceleration at any instant in time do not change as a function of distance from the substratum. Thus, we have assumed that the kinematics of the flow encountered by an organism are independent of body size. Clearly, this assumption is violated in some situations, as discussed below. However, we believe this assumption to be a valid first approximation for solitary organisms for the following reasons.

1) The establishment of a boundary layer requires time. Is there sufficient time during the onrush of a turbulent bore for viscosity to result in the buildup of a significantly large boundary layer? This question is not relevant to "steady" turbulent flows. We use an example provided by Schlichting (1979): the growth of a turbulent boundary layer from the leading edge of a flat plate. The boundary layer thickness, δ , is defined as the distance above the substratum at which the velocity is 99% of free-stream velocity. Schlichting gives an equation that relates boundary layer thickness to the distance x of a point from the leading edge of a flat plate:

$$\delta = 0.37x(Ux/\nu)^{-0.2}, \quad (15)$$

where U is the free-stream velocity and ν is the kinematic viscosity. If we consider a bulk of fluid moving with speed U towards a point on a flat rock wall, we may estimate the growth (over time) of the boundary layer at that point by equating x to Ut , where t is the elapsed time. Thus, Eq. 15 becomes:

$$\delta = 0.37U^{0.6}t^{0.8}\nu^{0.2}. \quad (16)$$

Using Fig. 4 to provide numerical estimates of the values in the above equation, and assuming a kinematic viscosity of 10^{-6} m²/s, we calculate that the boundary layer would build up to its maximum thickness of only 5×10^{-3} m in ≈ 0.05 s, when $U = 5$ m/s. Of course, the time-averaged value of δ encountered by an organism would be lower than this estimate of maximum δ . Thus, the height above the substratum at which water velocity reaches 99% of free stream is only a fraction of the height of most organisms encountered in this study.

2) A velocity gradient exists within a boundary layer. The crucial feature for our analysis is not how thick the boundary layer is but whether there is a significant change in the overall velocity as an organism grows taller. While for similar free-stream velocities, turbulent boundary layers are thicker than laminar ones, they have, in general, blunter profiles; the steepest velocity gradient is confined to the region near the substratum; from this region outwards, the change in velocity is quite small. At only 5% of the way up into the boundary layer, the local velocity is already $> 50\%$ of the free-stream velocity. From 20% of the boundary layer thickness outwards, the velocity changes only by $\approx 25\%$ (see Schlichting 1979: Fig. 18.5). Consequently, our assumption of a constant velocity is reasonable for turbulent boundary layers even as thick as 1–2 cm. Thus, owing to the very short duration of the initial surge and to the nature of turbulent boundary layer profiles, our assumption that the flow encountered by macroscopic solitary organisms is independent of body size appears valid.

The force trace from one large breaking wave is shown in Fig. 4, along with the water velocities and accelerations calculated to be responsible for the force. The velocity at maximum acceleration cannot be precisely predicted for waves in general and, indeed, for the 30 waves for which calculations were made, no significant correlation exists between maximum acceleration and the velocity at which that acceleration occurred ($r = 0.022$, $N = 30$, $P > .5$).

DEVELOPMENT OF THE MODEL

The hydrodynamic forces that act on a simple representation of a wave-swept organism are illustrated in Fig. 5. The organism is represented by a hemisphere of radius L_r , attached to a planar surface. The passage of a wave causes water to flow along the surface past the organism, resulting in a number of forces on the body. F_{df} , the force in the direction of flow (parallel to the surface plane), has two components: F_d , the drag due to the instantaneous velocity of the water, and F_a , the acceleration reaction due to the water's acceleration. From a rearrangement of Eq. 7 it can be seen that F_d varies with velocity, U :

$$F_d = 0.5\rho C_d A_p U^2. \quad (17)$$

Thus, for the hemisphere, where $A_p = 0.5\pi L_r^2$,

$$F_d = 0.25\rho C_d \pi L_r^2 U^2. \quad (18)$$

The accelerational component is

$$F_a = \rho C_m V dU/dt = (2/3)\rho C_m \pi L_r^3 dU/dt, \quad (19)$$

where V is the volume of the hemisphere ($(2/3)\pi L_r^3$). C_m for a hemisphere was measured to be 1.35. Both F_d and F_a are assumed to be applied at the centroid of the projected area, i.e., along the midline and, in the case of a hemisphere, a distance $4L_r/(3\pi)$ up from the base.

In addition to F_a and F_d which act only along the line of flow, the organism experiences lift, F_l , a force at right angles to the flow and away from the surface. Lift varies with water velocity in a manner similar to drag:

$$F_l = 0.5\rho C_l A_b U^2 = 0.5\rho C_l \pi L_r^2 U^2, \quad (20)$$

where A_b is the basal area of the model (πL_r^2). As mentioned above, lift is not centered on area A_b , but rather acts as a point force at the center of pressure, some distance downstream from the center of the base. For hemispheres attached to walls, lift has not been sufficiently studied to allow precise location of the center of pressure, but assuming that the hemisphere behaves similarly to the cones measured, the lift acts through a point along the midline and approximately $0.24 L_r$ downstream of center. As shown in Appendix 2, minor variations in the exact point of application of lift do not substantially affect our calculations.

If an organism is to remain stationary and attached to the surface plane, the forces F_w , F_d , and F_l must be resisted by the adhesive substance that holds it in place. The forces acting on the adhesive are of two sorts. F_a and F_d tend to push the organism along the plane, shearing the adhesive. The average shear stress ($\bar{\sigma}_s$) is thus $(F_a + F_d)/A_b$. For a circular cross section, shear stress varies across the basal area and reaches a maximum at the center (Timoshenko and Gere 1972):

$$\sigma_{s,max} = 4\bar{\sigma}_s/3. \quad (21)$$

After substitution, Eq. 21 yields:

$$\begin{aligned} \sigma_{s,max} &= (4/3)(F_d + F_a)/A_b \\ &= (1/3)\rho C_d U^2 + (8/9)\rho C_m L_r dU/dt \\ &= K_1 \rho U^2 + K_2 \rho L_r dU/dt. \end{aligned} \quad (22)$$

The size of the organism, expressed for a hemisphere as its radius L_r , thus affects the maximum shear stress by affecting the acceleration reaction; for a given velocity and acceleration, the larger the organism the greater the shear stress on its basal adhesive.

In addition to a tendency for an organism to slide sideways in response to a shear force, there is a tendency, as shown in Fig. 5, for it to be overturned, usually in a direction such that its upstream edge is lifted and its downstream edge is forced down. This

tendency is due to the moment M_1 applied by the shear force acting some distance above the base. This overturning moment is counteracted to some degree by the moment M_2 due to the lift force acting downstream of the center of the organism. Unless $M_1 = M_2$ there is some net tendency for rotation about the neutral axis. The neutral axis is a line in the plane of the base perpendicular to the direction of flow and passing through the center of the base. If $M_1 > M_2$, this rotation extends the adhesive on the upstream half of the base and compresses the adhesive on the downstream half. If $M_1 < M_2$, the opposite happens. The adhesive at the neutral axis is neither compressed nor extended. The net moment ($M_1 - M_2$) thus exerts a stress on the adhesive in a direction *normal* to the basal plane. The magnitude of this normal stress, σ_n , varies with the distance, d , from the neutral axis (Timoshenko and Gere 1972):

$$\sigma_n = (M_1 - M_2)d/I, \quad (23)$$

where I is the second moment of area about the neutral axis. For a circular cross section, as in a hemisphere, $I = 0.25\pi L_r^4$. The normal stress thus reaches a maximum at the leading and trailing edges, where $d = L_r$. In addition to the normal stress due to the net moment, there is a normal stress placed directly on the adhesive by the lift. This normal stress tends to change the location of the neutral axis within the model to a position downstream of center (Timoshenko and Gere 1972), but unless F_l is large compared to F_d (and it is not for the bodies we studied), the effect is minor, so it has not been included in this analysis. Thus, the maximum normal stress, $\sigma_{n,max}$, is:

$$\sigma_{n,max} = (F_l/A_b) + (M_1 - M_2)L_r/I. \quad (24)$$

Substitution in Eq. 24 and rearrangement yield:

$$\begin{aligned} \sigma_{n,max} &= 0.5\rho C_l U^2 - 0.472\rho C_l U^2 \\ &\quad + [4/(3\pi)]\rho C_d U^2 \\ &\quad + [32/(9\pi)]\rho C_m L_r dU/dt \\ &= K_3 \rho U^2 - K_4 \rho U^2 + K_5 \rho U^2 \\ &\quad + K_6 \rho L_r dU/dt \\ &= U^2 \rho (K_3 - K_4 + K_5) \\ &\quad + K_6 \rho L_r dU/dt. \end{aligned} \quad (25)$$

As with the maximum shear stress, the maximum normal stress for a given velocity and acceleration is affected by the size of the organism; the larger the radius, the greater the value of $\sigma_{n,max}$. From Eqs. 22 and 25 it can be seen that $L_{r,max}$, a measure of the maximum size is, if due to constraints of shear stress:

$$L_{r,max} = (\sigma_{s,max} - K_1 \rho U^2)/(K_2 \rho dU/dt), \quad (26)$$

or, if due to constraints of normal stress:

$$L_{r,max} = [\sigma_{n,max} - U^2 \rho (K_3 - K_4 + K_5)] / (K_6 \rho dU/dt). \quad (27)$$

TABLE 2. Shape constants for various standard shapes.

	Hemisphere	Cone	Cylinder
K_1	$(1/3)C_d$	$(2/3\pi)B^*C_d$	$(4/3\pi)BC_d$
K_2	$(8/9)C_m$	$(4/9)BC_m$	$(4/3)BC_m$
K_3	$(1/2)C_l$	$(1/2)C_l$	$(1/2)C_l$
K_4	$-0.472C_l$	$-0.472C_l$	$-0.472C_l$
K_5	$(4/3\pi)C_d$	$[(2-2^{1/2})/\pi]B^2C_d$	$(2/\pi)B^2C_d$
K_6	$(32/9\pi)C_m$	$(4/3\pi)B^2C_m$	$2B^2C_m$

* B = height/radius.

In the second case the adhesive will in all likelihood fail in tension, most materials being much stronger in compression than in tension (Wainwright et al. 1976). The maximum size of an organism (or representation) thus depends on:

- 1) the strength of the structure or the adhesive holding the structure in place,
- 2) the velocity of the water, and
- 3) the water's acceleration. These parameters can be empirically measured and used to examine critically the maximum sizes of organisms inhabiting wave-swept environments.

The various constants derived here for a hemisphere (K_1 to K_6) have also been derived for other shapes such as cones and cylinders, and these values are shown in Table 2.

For certain organisms, some of the forces described above are negligible, and for these organisms a simplified analysis suffices. For example, consider a plate-like organism such as the fire coral *Millepora complanata*, extending perpendicularly out of a planar surface. If the height of the organism, L_h , is much greater than its depth, the length of the moment arm ($M = L_h/2$) is such that the normal forces exerted at the edges of the base far exceed the shear force. The shear force may thus be neglected. Similarly, for such an organism, C_l is approximately zero (Hoerner and Borst 1975). Further, the organism has a very small area over which lift can act. Thus, we may neglect lift forces in the calculation of size:

$$F_{dr} = 0.5\rho C_d W L_h^2 U^2 + \rho C_m W T L_h^3 dU/dt, \quad (28)$$

where W and T are the ratio of the width of the plate and thickness of the plate, respectively, to L_h . Then

$$\sigma_{n,max} = M y/I \\ = 3(\rho/2T^2) C_d U^2 + 3(\rho/T) C_m L_h dU/dt, \quad (29)$$

where M is the bending moment, y is the distance from the neutral axis ($1/2$ the thickness), and I is the second moment of area ($[1/12]W T^3 L_h^4$). Similar calculations may be made for organisms shaped like long, thin cylinders, and the appropriate constants are listed in Table 2.

One final and important addition must be made to these sets of equations before they can be productively applied to "real world" situations. As stated previously, the maximum size of an organism in a certain

flow situation is a function of the strength of some critical structure in the organism. If all individuals of a certain species have the same breaking strength, all have the same mechanical limitation. However, some distribution of breaking strengths is to be expected, and for the organisms we examined, this distribution was indistinguishable from a normal distribution (analysis by graphical method; Zar 1974). We assume that breaking strength (force per unit area required to break a material) is independent of size. Thus, the breaking strength distribution of each species may be characterized by a mean and a standard deviation, and for a population of organisms the fraction having a breaking strength of at least a certain magnitude, σ' , can be specified:

$$P_s = 1 - \int_0^{\sigma'} s^{-1}(2\pi)^{-1/2} \\ \cdot \exp - [(\sigma - \bar{\sigma})^2/2s^2] \cdot d\sigma, \quad (30)$$

where s is the standard deviation, and $\bar{\sigma}$ is the mean breaking stress (Zar 1974). Thus P_s is the fraction of the population that, on average, is not dislodged when a stress, σ' , is applied to each organism. Conversely, $P_d (= 1 - P_s)$ is the fraction of the population that does not have the adhesive strength to resist dislodgement by a wave with a given set of flow parameters.

Alternatively, P_s and P_d may be viewed as estimates of the probability of survival or dislodgement, respectively, for an individual chosen at random from the population. Because natural selection acts on the individual rather than a population, this second viewpoint is more relevant to the discussion at hand.

The cumulative probability of survival or dislodgement, $P_{s,cum}$ or $P_{d,cum}$, respectively, can be calculated:

$$P_{s,cum} = (P_{s_1} \times P_{s_2} \times \dots \times P_{s_N}) \\ P_{d,cum} = 1 - (P_{s,cum}), \quad (31)$$

where P_{s_i} is the probability of not being dislodged by wave i and N is the number of waves encountered. Note that Eq. 31 requires that the flow parameters of each of the N waves be known. Further, because each wave dislodges individuals, the parameters of the breaking stress distribution for the remaining individuals may vary from one wave to the next. Thus, while correct as written, Eq. 31 is difficult to apply. Methods for approximating Eq. 31 are discussed below (Discussion: P_d , $L dP_d/dL$, and Natural Selection).

It is unlikely that (without actually being dislodged) an organism can determine its instantaneous position on its species' breaking strength distribution. Once dislodged, it is too late to act on the information. Thus it would be adaptive for an organism not to grow beyond the size range in which, for given flow parameters, its cumulative probability of dislodgement is acceptably low. The definition of what constitutes an acceptably low probability is dealt with in the Discussion.

Note that the probability of dislodgement is the sum of two component probabilities. From an examination

of Eq. 5 it can be seen that in theory even in steady flow ($dU/dt = 0$) a stress is present due to the drag force. This size- and acceleration-independent stress can be used in Eq. 30 to calculate a size-independent base probability of dislodgement, P_b . For an organism in accelerating flow there is a stress due to the acceleration reaction that increases the probability of dislodgement by an amount P_a , the accelerational component of the probability. Thus

$$P_d = P_b + P_a. \quad (32)$$

For an organism of a certain shape, exposed to a given set of flow parameters and having been chosen at random from a population with a certain distribution of breaking strengths, it is possible to calculate the increase in risk concomitant with an increase in size, dP_d/dL :

$$dP_d/dL = (dP_d/d\sigma') \cdot (d\sigma'/dL). \quad (33)$$

To calculate the increase in risk of dislodgement by shear stress, Eq. 22 can be used:

$$\begin{aligned} d\sigma'/dL &= d(K_{2\rho}L_r dU/dt + K_{1\rho}U^2)/dL \\ &= K_{2\rho} dU/dt; \end{aligned} \quad (34)$$

or, for the increase in risk of dislodgement by normal stress, Eq. 25 can be used:

$$\begin{aligned} d\sigma'/dL &= d[U^2\rho(K_3 - K_4 + K_5) \\ &\quad + K_{6\rho}L_r dU/dt]/dL \\ &= K_{6\rho} dU/dt, \end{aligned} \quad (35)$$

assuming $dC_d/dRe = 0$. From Eq. 30,

$$\begin{aligned} dP_d/d\sigma' &= d \left\{ \int_0^{\sigma'} s^{-1}(2\pi)^{-1/2} \right. \\ &\quad \cdot \exp - [(\sigma - \bar{\sigma})^2/2s^2] \cdot d\sigma' \left. \right\} / d\sigma' \\ &= s^{-1}(2\pi)^{-1/2} \exp - [(\sigma - \bar{\sigma})^2/2s^2]. \end{aligned} \quad (36)$$

Therefore, if we are considering shear stress,

$$\begin{aligned} dP_d/dL &= s^{-1}(2\pi)^{-1/2} \\ &\quad \cdot \exp - [(\sigma - \bar{\sigma})^2/2s^2] \cdot (K_{2\rho} dU/dt); \end{aligned} \quad (37)$$

or, if considering normal stress,

$$\begin{aligned} dP_d/dL &= s^{-1}(2\pi)^{-1/2} \\ &\quad \cdot \exp - [(\sigma - \bar{\sigma})^2/2s^2] \cdot (K_{6\rho} dU/dt). \end{aligned} \quad (38)$$

Eqs. 37 and 38 specify the change in P_d per unit change in absolute length. Of more interest is the change in P_d per unit change in relative length. This is:

$$dP_d/(dL/L) = L dP_d/dL. \quad (39)$$

For shear stresses,

$$\begin{aligned} L dP_d/dL &= s^{-1}(2\pi)^{-1/2} \\ &\quad \cdot \exp - [(\sigma - \bar{\sigma})^2/2s^2] \cdot LK_{2\rho}(dU/dt), \end{aligned} \quad (40)$$

or, for normal stresses,

$$\begin{aligned} L dP_d/dL &= s^{-1}(2\pi)^{-1/2} \\ &\quad \cdot \exp - [(\sigma - \bar{\sigma})^2/2s^2] \cdot LK_{6\rho} dU/dt. \end{aligned} \quad (41)$$

By examining Eqs. 39, 40, and 41, it can be seen that $L dP_d/dL$, the size-specific increment in risk, is greatest when:

- 1) K_2 or K_6 is large (i.e., when C_m , the inertia coefficient, is large),
- 2) s is small (i.e., when there is a narrow range of breaking strength in the population),
- 3) L is large (i.e., when the absolute size of the organism is large), and

4) the stress on the organism is equal to the mean breaking stress. For a given set of flow parameters, $\sigma = \bar{\sigma}$ for a particular length, and the factor $\exp - [(\sigma - \bar{\sigma})^2/2s^2]$ decreases at lengths either longer or shorter.

If for a given flow regime this size-specific increment in risk is large, an animal would, by increasing its size, be exposing itself to a substantial increase in P_d , the probability of dislodgement by any given wave. In such a case it can be reasonably hypothesized that individual size in the species involved may, through the operation of natural selection, have been limited by mechanical factors. The strength of the selection pressure setting a limit to size depends on the relative disadvantage of increasing P_d as compared to the increase in fitness concomitant with an increase in size. A detailed examination of this interplay is postponed to the Discussion. However, at this point it is useful to choose a cutoff value above which $L dP_d/dL$ is considered large. For reasons treated more fully in the Discussion a value of $L dP_d/dL > 0.1$ is considered to be large enough to have limited the size of an organism.

APPLICATIONS OF THE MODEL

We used our model to investigate mechanical size restrictions in a variety of organisms. First we describe four cases for which we found evidence of such constraints: sea urchins, limpets, mussels, and one species of hydrocoral. Then we describe contrasting results for three snail species and three acorn barnacle species. Maximum observed sizes of these organisms are given in Table 3.

Sea urchins

The body of *Strongylocentrotus purpuratus*, the common purple urchin of the Pacific Northwest, consists of a roughly hemispherical rigid test (up to ≈ 0.07 m diameter) from which numerous spines protrude. On fully exposed shores individuals generally restrict themselves to shallow "burrows" worn into the rock surface and thus, presumably, avoid the full brunt of wave forces. However, on shores that are subject to lesser wave action (e.g., Shi-Shi Beach), urchins are found fully exposed to the forces of the prevailing waves, and are thus suitable for this analysis.

TABLE 3. Approximate maximum sizes for organisms used in this study.

Species	Dimension	Length
<i>Semibalanus cariosus</i>	L_r	1.85×10^{-2} m
<i>Balanus glandula</i>	L_r	1.00×10^{-2} m
<i>Balanus nubilis</i>	L_r	4.75×10^{-2} m
<i>Collisella digitalis</i>	L_r	0.85×10^{-2} m
<i>Collisella pelta</i>	L_r	1.50×10^{-2} m
<i>Notoacmaea scutum</i>	L_r	1.50×10^{-2} m
<i>Mytilus californianus</i>	L_r	11.0×10^{-2} m
<i>Strongylocentrotus purpuratus</i>	L_r	3.70×10^{-2} m
<i>Millepora complanata</i>	L_h	14.0×10^{-2} m
<i>Thais emarginata</i>	L	2.00×10^{-2} m
<i>Thais canaliculata</i>	L	2.00×10^{-2} m
<i>Liittorina scutulata</i>	L	0.50×10^{-2} m

Calculations were made for *S. purpuratus* from Shishi Beach using the C_d and C_m values shown in Table 1 and considering constraints of shear stress (Eq. 22).

Fig. 6 shows a plot of P_d vs. acceleration for four water velocities (1, 5, 10, and 20 m/s). At 10 and 20 m/s the urchins are exposed to high base probabilities of dislodgement, indicating that at these velocities a fully exposed organism would be dislodged regardless of its size. At the lower velocities presumably found in their semi-exposed habitats (1–5 m/s), the base probability of dislodgement is low (<.1), but the size-specific increment in P_d is large (>.3) (Fig. 6b, c). Thus, if these animals experience flows between 1 and 5 m/s their size may be limited by mechanical constraints.

Limpets

Limpets are small herbivorous gastropods with characteristic conical shells found attached to intertidal rocks on wave-swept shores. During low tides and when disturbed, a limpet clamps its shell tightly against the rock substratum. At high tide, however, when water flow is greatest, these animals move around to browse algae. Appropriate C_d , C_m , and C_l values and values defining the distribution of adhesive tenacities are shown in Table 1. Eq. 22 (for shear stress) was used for *C. digitalis*; Eq. 25 (for normal stress) for *C. pelta* and *N. scutum*. M. W. Denny (*personal observation*), at Friday Harbor, found that the stress necessary for breaking *C. digitalis* by shearing did not differ significantly from that by deformation applied in a normal direction. If the normal and shear tenacities of the open-coast *C. digitalis* are also equal, our results for one will apply to both. Fig. 7a_i, b_i, c_i shows the P_d vs. acceleration curves for the three limpet species at four water velocities. It can readily be seen that stationary limpets, firmly clamped down (---), run little risk of being dislodged by wave forces. However, when the calculated breaking stress values for moving limpets are used in the calculations (—), predictions of both the base probability of dislodgement and the size-specific in-

crement in risk are much higher. This is more obvious for *C. pelta* and *N. scutum* (see Fig. 7a, b). The tenacity of *C. digitalis* is greater than that of either *C. pelta* or *N. scutum*, and its size is smaller, hence for this species

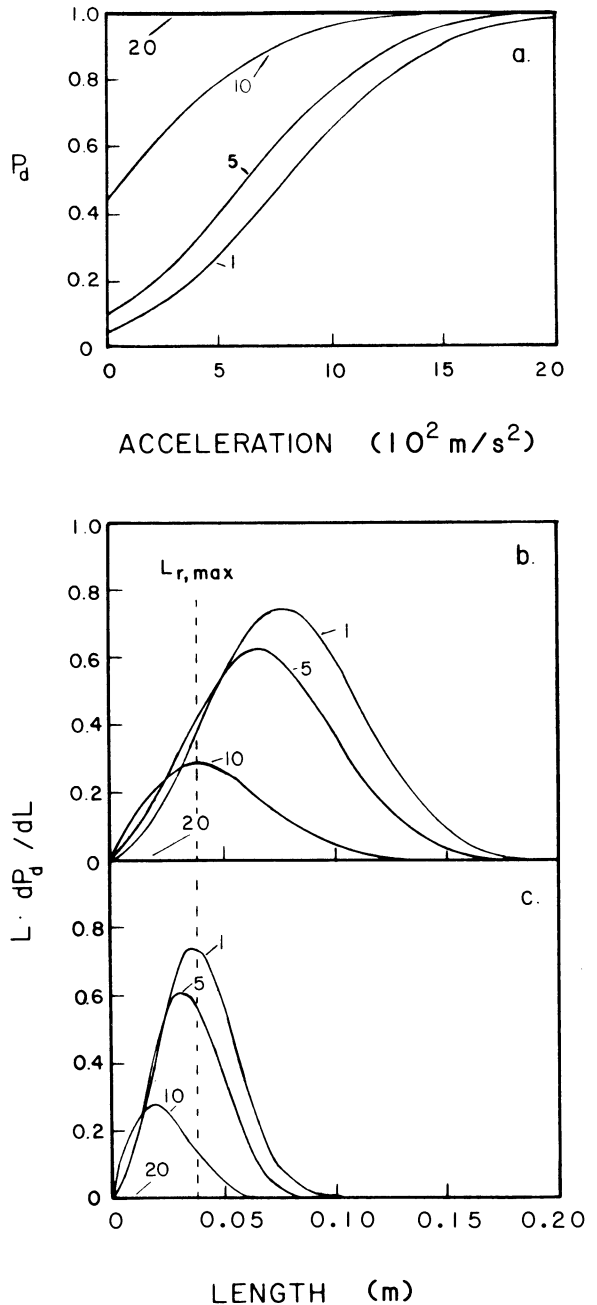


FIG. 6. Predictions for the urchin *Strongylocentrotus purpuratus* exposed to a variety of water velocities (1, 5, 10, and 20 m/s). (a) Probability of dislodgement (P_d) plotted against water acceleration (urchin is of maximum radius, $L_{r,max} = 0.037 \text{ m}$). (b, c) The size-specific increment in risk ($L \cdot dP_d / dL$) plotted against size L_r (radius of urchin) for an animal exposed to (b) 500 m/s^2 and (c) 1000 m/s^2 . The maximum observed size is shown by the vertical dashed line.

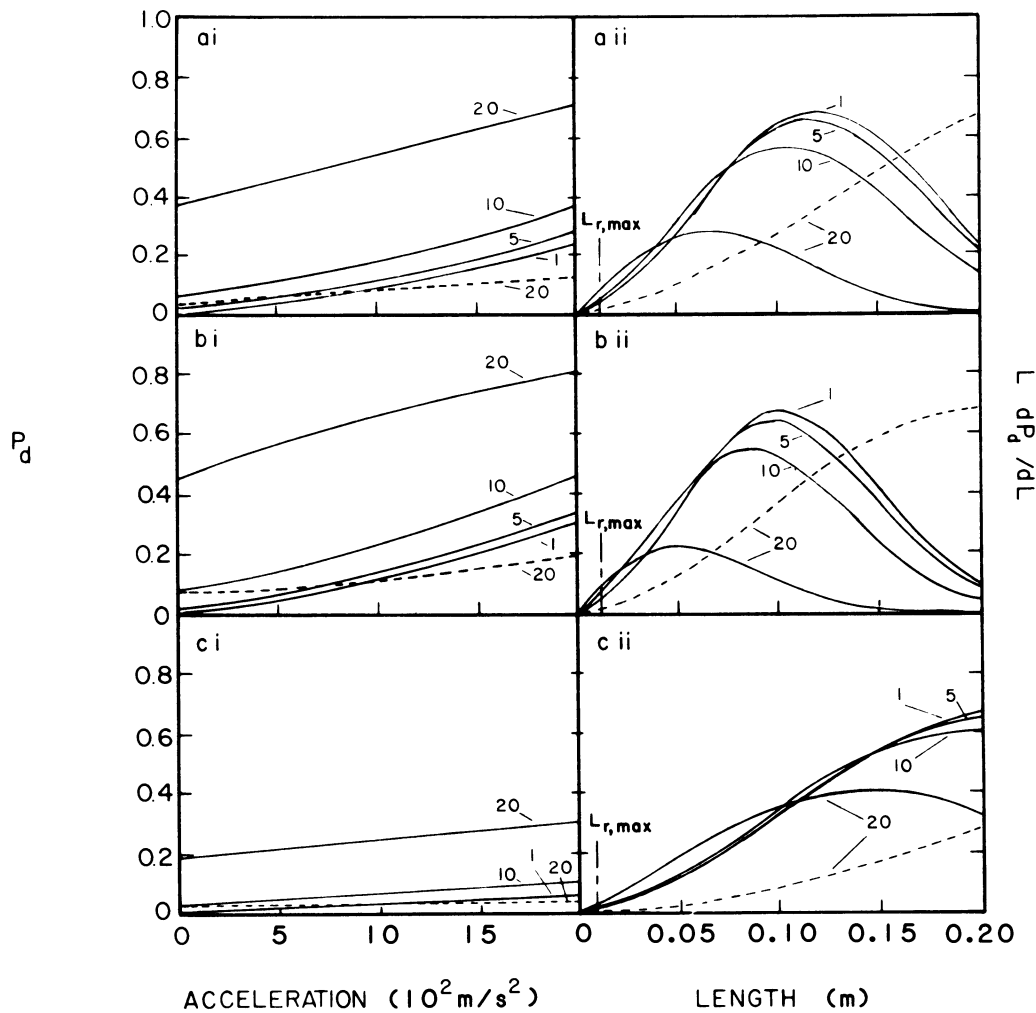


FIG. 7. Predictions for the limpets *Colisella pelta* (a), *Notoacmaea scutum* (b), and *Colisella digitalis* (c) exposed to a variety of water velocities (1–10 m/s). Predictions are based on adhesive tenacities for moving (—) and stationary (---) limpets. Left panels: probability of dislodgement (P_d) plotted against water acceleration for limpets of the observed maximum size (radius $L_{r,max}$). Right panels: the size-specific increment in risk ($L dP_d/dL$) plotted against size (radius) for limpets exposed to a water acceleration of 500 m/s^2 . The observed maximum size is shown by a vertical broken line.

$L dP_d/dL$ and P_b are both lower. Note that at a very high water velocity (20 m/s) the base probability of dislodgement is high (>0.35) for *C. pelta* and *N. scutum*. At such high flow rates these two species would of necessity have to stop moving (and thereby stop feeding) if they were to have any reasonable chance of remaining attached. In contrast, *C. digitalis*, a more common limpet on very exposed shores at Tatoosh Island, has a considerably lower base risk even at the most extreme flow conditions. For each of the three species, a size increase to a length above that seen in nature would result in an increase in $L dP_d/dL$ (Fig. 7a ii, b ii, c ii). From these data we conjecture that at high flow rates ($>10 \text{ m/s}$) *C. pelta* and *N. scutum* may be mechanically limited to sizes at which the stress placed on an individual's adhesive is small enough that the decrease in adhesive tenacity that accompanies

feeding can be tolerated. At flow rates of 1–10 m/s the base probabilities are low (<0.1) and $L dP_d/dL$ is high (>0.1), so we hypothesize that *C. pelta* and *N. scutum* may be limited in size by mechanical factors.

Mussels

The common mussel of the Washington coast, *Mytilus californianus*, differs considerably in general morphology from urchins and limpets. Rather than having a shell closely applied to the substratum, with a large adhesive base, the mussel has a shell that protrudes well above the substratum and is held in place by an array of byssal threads. Despite this difference in morphology, the adhesive strength of *M. californianus*, relative to body volume and projected area, was found to be of a scale appropriate for our model (Eq. 22), and thus only minor rearrangements in the equations were

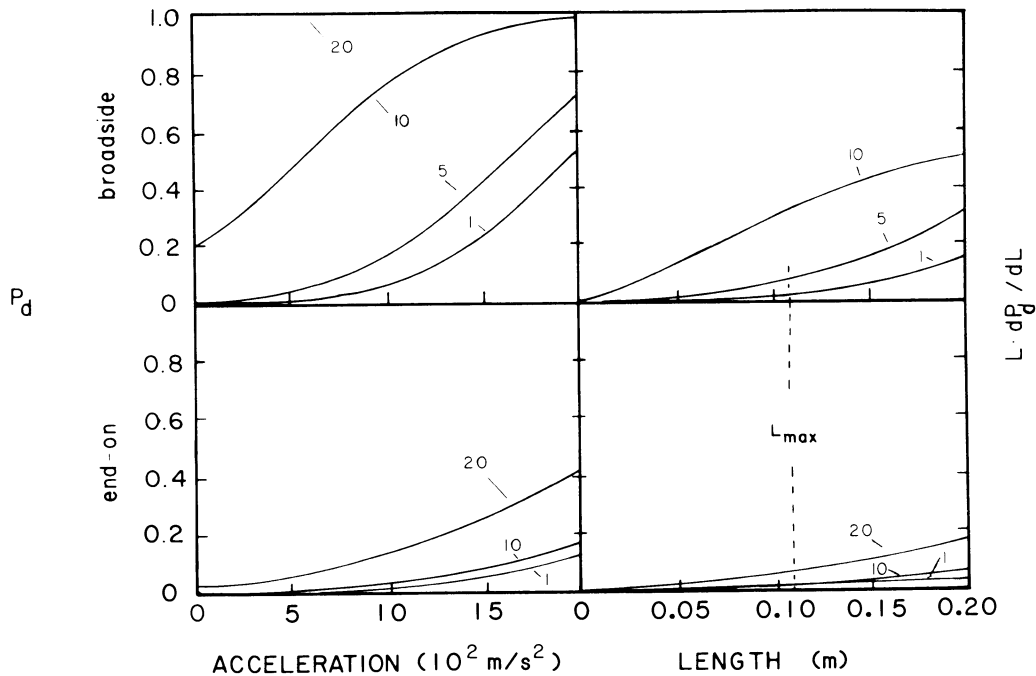


FIG. 8. Predictions for the mussel *Mytilus californianus* exposed to a variety of water velocities (1–20 m/s) oriented both broadside (upper panels) and end on (lower panels) relative to the direction of flow. Left panels: the probability of dislodgement (P_d) plotted against water acceleration for mussels of dimension L_{max} . Right panels: the size-specific increment in risk plotted against size for mussels exposed to a water acceleration of 500 m/s^2 . L_{max} is the maximum size of solitary mussels observed on Tatoosh Island, Washington.

necessary. The dislodgement force for *M. californianus* was expressed as an “equivalent stress,” σ_{eq} by dividing force by a calculated projected area, A_p . A_p (in square metres) varies with the direction of flow relative to the mussel’s long axis (L , in metres), and is at a minimum ($A_{p,min} = 0.126 L^{1.91}$) when flow is along the axis and a maximum ($A_{p,max} = 0.276 L^{1.91}$) when flow is perpendicular to the axis. The equation appropriate for calculating L_{max} is thus:

$$\sigma_{eq,max} = (0.5\rho C_d A_p U^2)/A_{p,min} + (\rho C_m V dU/dt)/A_{p,min}. \quad (42)$$

$A_p/A_{p,min}$ equals 1 when the mussel is end on to the flow and equals 2.19 when the mussel is broadside. As given in Materials and Methods: Size and Tenacity of Mussels, $V = 0.061 L^{2.86}$ (V in cubic metres, L in metres), so

$$\sigma_{eq,max} = 0.5\rho C_d A_p U^2/A_{p,min} + 0.48\rho C_m L dU/dt. \quad (43)$$

Values of P_d are shown in Fig. 8 as a function of acceleration. It can be seen that even at a relatively low velocity for this exposed environment (10 m/s), a mussel oriented broadside to the flow has a very high value of $L dP_d/dL$. Consequently, even at 10 m/s the size of a solitary mussel with this orientation would be severely limited by mechanical factors. At higher velocities the base probability of dislodgement approaches unity. Thus, solitary mussels oriented directly

broadside to the prevailing flow appear to be mechanically unlikely beasts, and indeed they are very seldom found. An orientation end-on to the flow is more feasible (Fig. 8), since, even at high velocities (20 m/s), both the base probability and size-specific increment in risk are low. If water moved only along one axis these appropriately oriented mussels would be at little risk from the flow; however, in breaking waves the unpredictable, turbulent nature of flow renders accurate orientation unlikely except in surge channels, where the direction of flow is more predictable. Indeed, mussels were found oriented in a direction parallel to flow in such habitats on Tatoosh Island. For mussels exposed neither end on nor broadside to the flow, the forces encountered are intermediate between broadside and end-on values, and P_d and $L dP_d/dL$ likewise are intermediate. As with the organisms discussed above, the size-specific increment in risk for *M. californianus* would increase if the animal increased to a size above those observed in the field (Fig. 8).

Coral

Millepora complanata, one of the “fire corals” of the western Caribbean, is a platelike hydrocoral that inhabits the surf zone of reefs. At Galeta Point the plates grow perpendicular to the substratum and are generally oriented broadside to the prevailing flow of breaking waves. *M. complanata* typically grows at depths of 0–

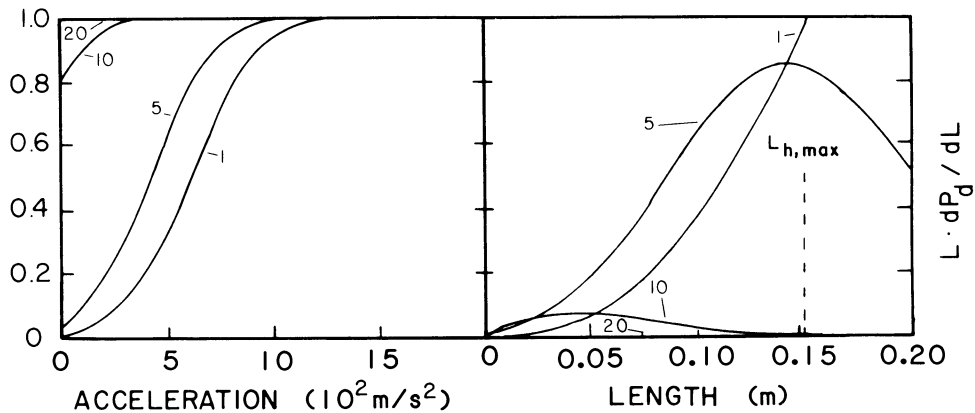


FIG. 9. Predictions for the fire coral *Millepora complanata* exposed to a variety of water velocities (1–20 m/s). Left panel: the probability of breaking plotted against water acceleration for a coral of blade length $L_h = 0.14$ m. Right panel: the size-specific increment in risk plotted against blade length for a coral exposed to a water acceleration of 500 m/s^2 . $L_{h,max}$ is the maximum observed blade length.

4 m and is thus routinely exposed to the large accelerations and velocities accompanying breaking waves.

For this coral the thickness of the plate at the base is 0.130 times the height, L_h . Appropriate values for $C_d (=1.8)$ and $C_m (=6)$ have been taken from the studies of flat plates by Keulegan and Carpenter (1958), and these values have been inserted into Eq. 29 to calculate stress. Using these stress values the curves of P_d and $L \cdot dP_d/dL$ have been calculated for various velocities and accelerations (Fig. 9).

At velocities that are high for this reef environment ($> 10 \text{ m/s}$), the base probability of dislodgement is very high (> 0.8), but it is unlikely that waves high enough to cause such velocities ($> 5 \text{ m/s}$) occur at the site where $L_{h,max}$ was measured. For the maximum wave heights observed at Galeta Point (2–3 m; J. Cubit, *personal communication*) velocities of 7.5 m/s are more likely (Eq. 14). At these velocities the base probability is relatively low and $L \cdot dP_d/dL$ is high (> 0.2). On this basis, it seems likely that the size of *M. complanata* at Galeta Point may be limited by the mechanical consequences of accelerational flow. At other sites in the Caribbean, *M. complanata* forms plates in deeper water (2–4 m), but is present only as an encrusting form in the surf zone (S. Palumbi, *personal communication*). This difference in morphology may result from the mechanical limitations cited here.

Snails

Data for three species of snails commonly found on Tatoosh Island (*Thais [=Nucella] canaliculata*, *Thais emarginata*, *Littorina scutulata*) are shown in Table 1. Probability calculations have been made using Eq. 22 with the C_d and C_m values shown in Table 1. Compared to the tenacities of limpets, the stationary adhesive strength of these snails is quite low, with the consequence that at high water velocities (10–20 m/s) the size-independent probability of dislodgement ap-

proaches 1 (Fig. 10). At more moderate water velocities (1–10 m/s), the stationary adhesive strength of these animals is sufficient to result in a lower base probability. However, in the cases of *T. canaliculata* and *T. emarginata*, the decrease in tenacity associated with locomotion causes the size-independent probability of dislodgement for moving animals to approach 1 for velocities $> 5 \text{ m/s}$.

For all three species, at moderate flow conditions (5 m/s; $< 500 \text{ m/s}^2$) the $L \cdot dP_d/dL$ values based on stationary tenacity may be substantial. At mainstream velocities (10–20 m/s), or when the snails crawl while the water velocity exceeds 1 m/s, the size-specific increment in risk is quite low (< 0.01) at all accelerations due to the high base probability of dislodgement. Consequently, for the conditions that would be encountered by a moving animal exposed to even moderate flows, its risk of dislodgement is governed primarily by the size-independent probability of dislodgement. Thus, if the tenacity values measured by Miller (1974) are correct, we would predict that these snails are not capable of withstanding exposure to the velocities and accelerations accompanying breaking waves. This prediction is indeed born out, since these animals, while abundant on moderately exposed (*T. emarginata*) to fully exposed (*T. canaliculata*, *L. scutulata*) shores, confine themselves to microhabitats where they can avoid the prevailing flow. During periods of rapid water flow, *T. canaliculata* and *T. emarginata* on Tatoosh Island are typically found in crevices or nestled into the interior spaces of mussel beds, and *L. scutulata* are found hidden between acorn barnacles and in crevices in the rock surface. The environment may thus impose mechanical constraints on the behavior of these snails and indirectly limit their body size: they must remain small enough to utilize microhabitats not exposed to the full impact of breaking waves (sensu Kohn 1971; Emson and Faller-Fritsch 1976). Foraging is thus lim-

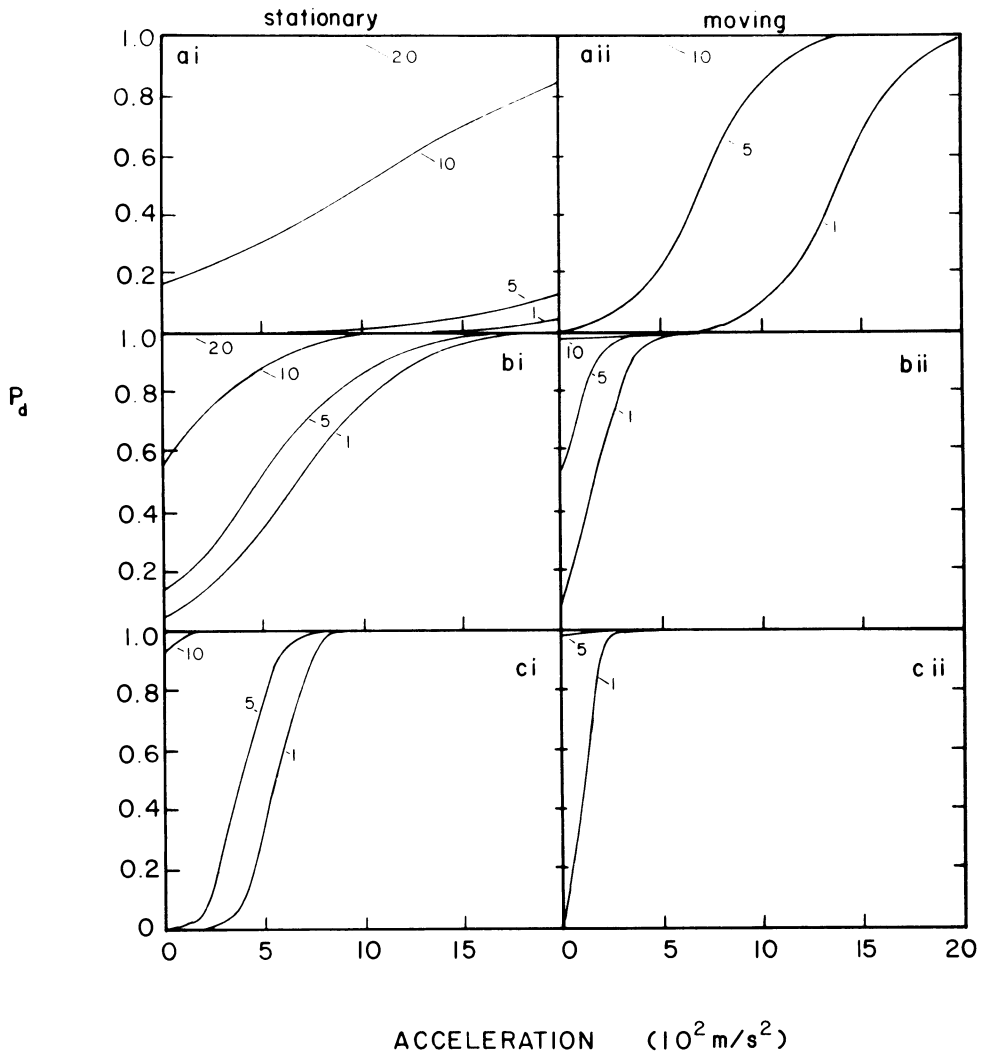


FIG. 10. Probability of dislodgement (P_d) plotted against water acceleration for stationary (left panels) and moving (right panels) snails exposed to a variety of water velocities (1–20 m/s). (a) *Littorina scutulata*, 0.005 m in length; (b) *Thais emarginata*, 0.02 m in length; (c) *Thais canaliculata*, 0.02 m in length. Notice that no animal can remain attached when exposed to a wave of 20 m/s.

ited to times when the environment is “mechanically safe.”

Acorn barnacles

The adhesive strengths of three species of acorn barnacle (*Semibalanus cariosus*, *Balanus glandula*, and *B. nubilus*) were measured on Tatoosh Island (Table 1). Probability calculations were made using the C_m and C_d values shown in Table 1 and using Eq. 22. The adhesive tenacity of these organisms is quite high; consequently the size-independent probability of dislodgement is low and the size-specific increment in risk even lower (see Fig. 11 for *S. cariosus*). It thus seems unlikely that the size of these organisms is limited by the mechanical factors considered here.

DISCUSSION

P_d , $L \frac{dP_d}{dL}$, and natural selection

We believe the theory and results presented here to be a reasonable description of the consequences of one wave interacting with a population of organisms. The conclusions drawn, however, rely on the argument that over the course of many waves large animals are removed at a rate sufficiently greater than that at which smaller animals are removed to cause a selection pressure towards smaller size. Thus, we argue that above a certain size an increase in size results in a decreased contribution to the next generation.

In order to justify these conclusions we must know something of the probability that an individual will

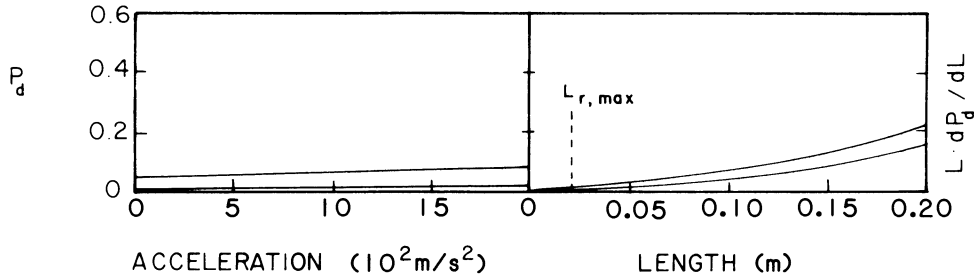


FIG. 11. Predictions for the barnacle *Semibalanus cariosus* exposed to water velocities of 1 and 20 m/s. Left panel: probability of dislodgement plotted against acceleration for a barnacle 0.018 m in radius. Right panel: size-specific increment in risk plotted against size (radius) for a barnacle exposed to a water acceleration of 500 m/s². The maximum radius observed is shown by the vertical dashed line.

survive to reproduce. Eq. 31 presents a method for the exact solution to the probability of survival, but, as noted, is difficult to apply in that it requires a knowledge of the velocity and acceleration accompanying each of the many waves that will occur before the organism reproduces. Our present knowledge of the long-term distribution of velocities and accelerations occurring in various microhabitats on exposed shores is not adequate to allow for a precise application of Eq. 31. It is possible, however, to use approximate forms of Eq. 31 as tools for comparing survivorship for organisms of various sizes. These approximations differ for motile and sessile organisms, depending on how much information can be obtained about an individual's adhesion to its substratum.

Motile organisms.—When a motile organism such as a limpet or snail moves, the status of its adhesion to the substratum is constantly changing; it may crawl over a bit of debris or an air bubble and thus become less strongly adherent, or it may crawl over a clean rock surface and adhere quite well. We assume here that the adhesive tenacity of an individual at one time is independent of tenacity at another time, but that as the organism crawls, its adhesive tenacity always lies within the instantaneous distribution shown by its species at that site. The latter is due both to variation among individuals in the strength of their “glue” and to variation in the substratum to which they are glued. Thus, for times short enough that growth can be neglected, the probability of an individual not being dislodged by a wave of given parameters is independent of time and equal to P_s (Eq. 31).

We can estimate the probability that a motile individual will survive a period of time over which it will be struck by N waves. For a certain wave, assume that the probability of encountering a velocity within a certain range, U_i , is P_{U_i} , and the probability of encountering an acceleration within a certain range, A_i , is P_{A_i} . Further assume, as suggested by the data cited earlier, that there is no correlation between the velocity and acceleration encountered. Under these assumptions, the number of waves with both velocity and accelera-

tion within these ranges is $NP_{U_i}P_{A_i}$. Eq. 31 can thus be approximated as

$$P_{s,cum} = (P_s)^{NP_{U_i}P_{A_i}} \times (P_s)^{NP_{U_i}P_{A_i}} \dots \times (P_s)^{NP_{U_{max}}P_{A_{max}}} \tag{44}$$

for the total range of velocities and accelerations between U_1 and U_{max} and A_1 and A_{max} . Each P_s can be evaluated, with Eq. 30, at the stress caused by the mean velocity and acceleration of the range applicable to each expression. Thus, Eq. 31 for the cumulative probability of survival can be rewritten:

$$P_{s,cum} = \exp N \sum_{i=1}^{imax} P_{U_i} \sum_{j=1}^{jmax} P_{A_j} \ln P_s \tag{45}$$

If the probability distributions of P_{U_i} and P_{A_i} are known, $P_{s,cum}$ can be evaluated. The distribution of P_{U_i} for intertidal habitats has not been measured, but sufficient information is known about waves in both deep and shallow water to arrive at an estimate. The height of waves in deep water approximately follows a Rayleigh distribution (United States Army Corps of Engineers 1977):

$$P_{(H>H')} = \exp -(H'/H_{rms})^2, \tag{46}$$

where $P_{(H>H')}$ is the probability that the wave height is greater than a value H' , and H_{rms} is the root-mean-square wave height measured over the N waves. The orbital velocity of water within a wave is a function of the wave height (see Eq. 14). If we assume that waves break near enough to shore that the velocity encountered by an organism on the shore is equal to the crest velocity at breaking (i.e., the bottom slope is steep), and that the wave breaks when its height is equal to 0.7 of the water depth (Wiegell 1964), Eq. 46 can be rewritten as

$$P_{(U>U')} = \exp - [(U')^2/(1.7 g H_{rms})^2], \tag{47}$$

where $P_{(U>U')}$ is the probability that the velocity is greater than U' . P_{U_i} can thus be approximated as

$$P_{U_i} = P_{(U>U')} - P_{(U>U'')}, \tag{48}$$

where U' and U'' are the ends of the range U_i , with

$U'' > U'$. In making these assumptions we ignore the increase in wave height as deep-water waves shoal.

We next must consider the probability of encountering a certain acceleration. P_A is unknown. Rather than assuming some probability function, we set the acceleration to a value of 500 m/s², assuming that at some point during wave breaking this value will be encountered. This acceleration is larger than most measured on Tatoosh Island, but as noted in Materials and Methods the measurements probably underestimate the true values. Eq. 45 thus becomes:

$$P_{s,cum} = \exp N \sum_{i=1}^{imax} P_{U_i} \ln P_s, \quad (49)$$

where P_s is evaluated for the mean velocity within each range U_i and for an acceleration of 500 m/s². Given values for H_{rms} , the hydrodynamic coefficients for the given organism, (C_d , C_b , C_m), the population distribution of breaking strengths, and the animal's size, we can calculate an approximation of the probability of surviving the impact of N waves.

Sessile organisms.—The approximation of Eq. 31 differs for sessile organisms. Eq. 49 is based on the assumption that the adhesive tenacity of the individual varies from one time to the next. While this assumption seems valid for moving limpets or snails, for an organism that is permanently cemented in place, such as an acorn barnacle, it seems more reasonable to assume that the adhesive tenacity of an individual is constant through time. This time-independence can be incorporated into an approximation of Eq. 31 as follows. Consider an individual of fixed, but initially unknown, adhesive tenacity. Before this individual is subjected to wave forces its adhesive tenacity is best estimated to lie within the distribution of adhesive tenacities shown by its species at the particular site being examined. In contrast to the situation for motile organisms, after the sessile individual survives N waves, information is available as to its adhesive tenacity. Each wave has subjected the organism to a stress, and the organism has not been dislodged. Therefore, the adhesive tenacity of the organism can be less than a certain value, σ' , only if every one of the N waves had a velocity and acceleration such that the stress placed on the organism was less than σ' . If, as assumed before, there is a fixed value for acceleration, the stress placed on the organism by each wave is determined solely by water velocity. We assume that the distribution of velocities is as described by Eq. 47. Thus the probability that each of N waves has a velocity less than U' is

$$[1 - P_{(U>U')}]^N, \quad (50)$$

and the probability that an organism has less than a certain breaking stress is

$$P_d [1 - P_{(U>U')}]^N. \quad (51)$$

For example, if $H_{rms} = 1.0$ m, the probability that a given wave has a velocity >0.1 m/s is very high ($>.99$).

Thus, $1 - P_{(U>U')}$ is nearly zero, and $[1 - P_{(U>U')}]^N$ is smaller still. Having encountered N waves and survived, the organism has a very low probability of having an adhesive strength incapable of withstanding the stress caused by a velocity of 0.1 m/s. Thus, the probability of surviving a wave with a velocity of 0.1 m/s is high. For organisms with a fixed value of σ' , the probability of surviving the impact of one wave after having already survived the impact of N waves can be determined:

$$P'_s = 1 - \{P_d[1 - P_{(U>U')}]^N\}. \quad (52)$$

Inserting this adjusted value of P'_s into Eq. 49 yields:

$$P'_{s,cum} = \exp \sum_{N=0}^M \sum_{i=1}^{imax} P_{U_i} \ln P'_s, \quad (53)$$

where M is the total number of waves encountered.

In this approximation of Eq. 31, P'_s is evaluated for each wave. An intertidal organism may encounter well over a million waves in a year, and calculating $P'_{s,cum}$ for a year's time would be extremely laborious. A further approximation can be made by re-evaluating P_s on a daily rather than a wave-by-wave basis:

$$P''_{s,cum} \cong \exp \sum_{D=0}^{Dmax} N \sum_{i=1}^{imax} P_{U_i} \cdot \ln(1 - P_d[1 - P_{(U>U')}]^{ND}) \quad (54)$$

where N is the number of waves per day and D is the number of days.

As approximations of the exact solution to survivorship (Eq. 31), Eqs. 49 and 54 can be used to compare survivorship of organisms of different sizes. This was done by assuming a constant value for H_{rms} and calculating $P_{s,cum}$ or $P''_{s,cum}$ as a function of time for organisms of the same species but different characteristic lengths. *It should be noted, however, that these calculated survivorship curves are intended only as a means to compare different-sized members of a species, not as an accurate calculation of actual survivorship on a real shore.* Several aspects of the approximation procedure must be refined or modified before accurate calculations of "real world" survivorship can be made. For example, (1) the H_{rms} of the sea varies widely from day to day and from site to site, (2) the approximation of P_{U_i} by a Rayleigh function based on deep-water wave height is simply an educated guess as to the true distribution of flows in the surfzone, and will undoubtedly have to be modified to apply directly to any specific site, (3) the possible effects of variation in acceleration have not been taken into account, and (4) the effects of the organism's growth or the possible deterioration of the adhesive have been ignored.

Figs. 12 and 13 show the results of applying these approximations to several of the species studied here. Because of their very high base probability of dislodgement, and the likelihood that their size is limited by

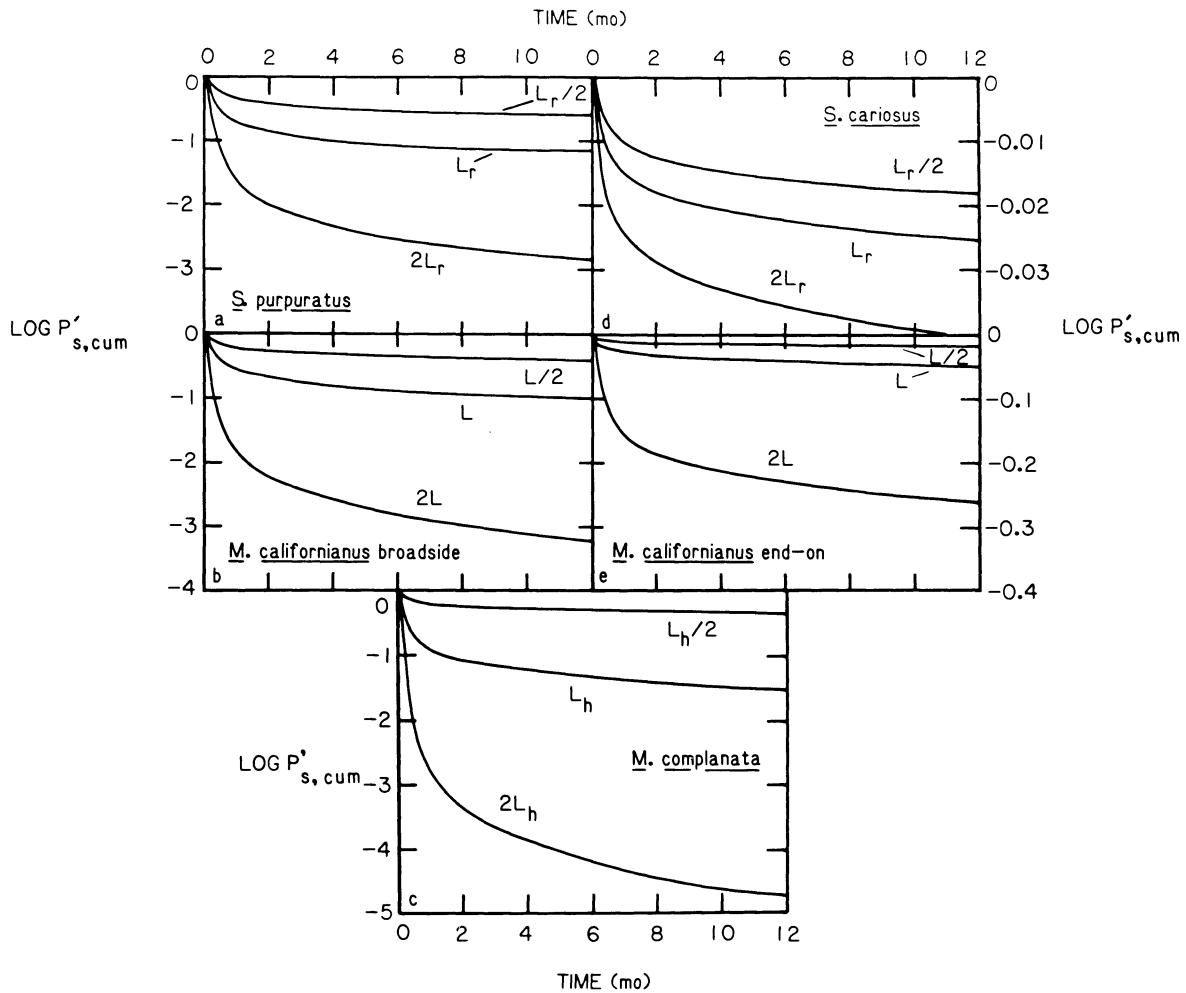


FIG. 12. The logarithm of the cumulative probability of survival ($P_{s,cum}$) plotted against time (in months) for a variety of intertidal organisms (the urchin *Strongylocentrotus purpuratus*, the barnacle *Semibalanus cariosus*, the mussel *Mytilus californianus*, and the coral *Millepora complanata*). For each animal, predictions were calculated using: the maximum observed size (L), half that size ($L/2$), and twice that size ($2L$).

other than mechanical factors, the snails *T. emarginata*, *T. canaliculata*, and *L. scutulata* were not included in this examination.

Animals were assumed to encounter 5000 waves/d. In general, a value of $H_{rms} = 1.0$ m was used, as suggested for exposed shores of the Pacific Northwest (United States Army Corps of Engineers 1977). For those species occurring in more protected areas (*S. purpuratus*, *M. complanata*), the value of H_{rms} was reduced accordingly (to 0.5 and 0.25 m, respectively). Except where noted, Eq. 54 (fixed adhesive tenacity) was used.

In order to examine whether mechanical factors are important selective pressures limiting the size of organisms in a particular population, one must compare the increase in reproductive output that accompanies an increase in size with the decrease in survivorship that accompanies that increase in size. A proper anal-

ysis of this question requires knowledge of the life histories (especially the age- and size-specific reproductive values) of the organisms being considered, as well as of the distribution in time of waves of different sizes impinging on a particular site. Although such information is not yet available for the animals under consideration, we present the following simple analysis to arrive at a "rule of thumb" for deciding whether mechanical factors are important in limiting the size of wave-swept organisms (i.e., for designating L dP/dL as "large" or "small").

For the sake of simplicity we assume that each organism produces young only once a year, and maintains a constant size throughout the year. For organisms that grow isometrically (as assumed for the animals studied here), a doubling in linear dimensions results in an eightfold increase in internal volume. We assume that this increase in volume is used to produce more

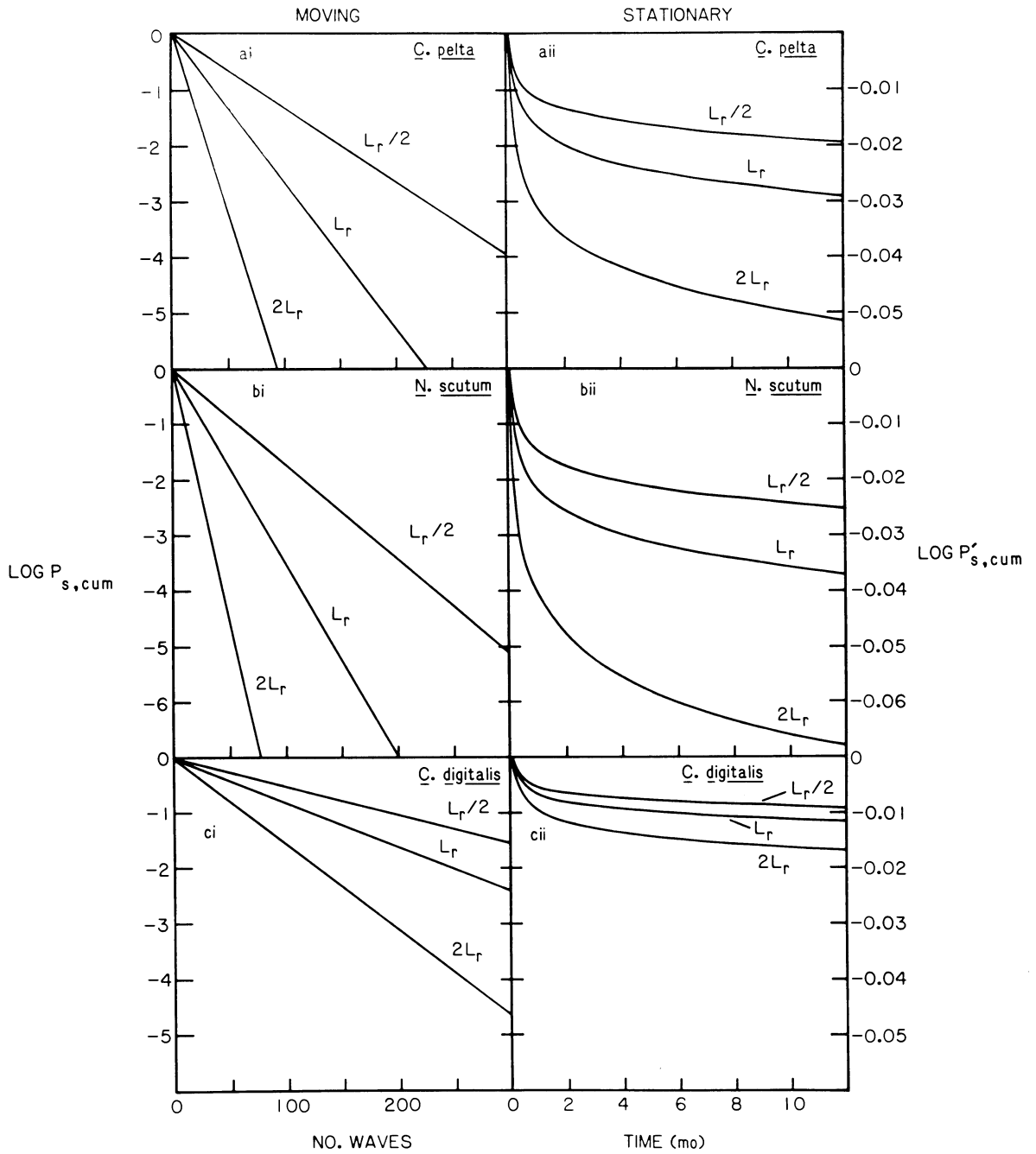


FIG. 13. The logarithm of the probability of survival plotted against number of waves encountered while moving (left panels) and against time while stationary (right panels) for three limpet species: (a) *Colisella pelta*, (b) *Notoacmaea scutum*, and (c) *Colisella digitalis*.

young or young of a greater viability, so that for each doubling in linear dimension, eight times as many progeny are contributed to the next generation. Under these assumptions, a selective pressure towards increased size should exist unless a doubling in linear dimension results in a greater than eightfold decrease

in survivorship to reproduction. In other words, if the survivorship ratio for an organism of one size relative to another member of that species twice that size exceeds eight, it is postulated that a selection pressure tending to limit size can exist due to the mechanical constraints examined here.

This is clearly a very simplified approach to the demographics of intertidal organisms; however, it is sufficient for our comparative purposes.

1. *A sea urchin, S. purpuratus*.—According to the predictions of the model urchins of the maximum size observed at Shi-Shi Beach are 41 times more likely to have survived to the end of a year than urchins of twice this size (Fig. 12a). Urchins half the maximum observed size have only a 3.8 times greater probability of survival than urchins of the maximum size. On the basis of the criterion established above, it appears feasible that mechanical factors exert a selection pressure limiting size in this urchin species.

2. *A mussel, Mytilus californianus*.—A mussel oriented broadside to the flow is 156 times more likely to survive to the end of one year at the maximum size observed on Tatoosh Island than at twice that size (Fig. 12b). A mussel half the observed maximum size is only 4.4 times as likely to survive as one at the maximum observed size. Thus, mussels oriented broadside to the flow may be limited by mechanical factors. However, if consistently oriented end on to the flow, a mussel of the observed maximum size is only 5.6 times as likely to survive as a mussel twice this size (Fig. 12e). Due to the unpredictable direction of flow in natural environments, any given mussel is oriented neither precisely end on nor precisely broadside to most waves. The appropriate survivorship ratio thus lies somewhere between 156 and 5.6 and is likely to be >8 . It seems reasonable to conclude that the size of solitary *M. californianus* is limited by mechanical factors.

3. *A coral, Millepora complanata*.—After only one month's exposure to waves with H_{rms} of 0.25 m, a coral blade of the maximum size observed on the Galeta reef is 90 times more likely to have remained intact than a blade twice that size (Fig. 12c). For survival to the end of a year this ratio is 1700. In contrast to the pattern for mussels and urchins, however, a coral blade that is half the observed maximum size is more likely to survive (≈ 16 times as likely) than a blade of the maximum observed size, and one might be led to conclude that there is selection pressure for this coral to be smaller than actually observed.

However, two factors must be taken into account when examining these results. (1) The reproductive output of *M. complanata* (when reproducing sexually) is probably more appropriately estimated as a function of the volume of polyps than of the volume of the entire plate. Assuming that polyps stay the same size but increase in number as the plate grows, the reproductive output of the colony should increase in proportion to the surface area of the plate, a fourfold increase for a doubling in length. (2) Unlike mussels and urchins, which in all likelihood die if dislodged (Dayton 1973), broken blades of *M. complanata* occasionally land on favorable substratum, re-attach, and grow (M. W. Denny, *personal observation*). Breakage may thus

serve as a dispersal mechanism (Highsmith 1982). These two factors lead to different possible interpretations of the results. If breakage results in death, the small increase in reproductive output with an increase in size for this colonial organism (relative to an individual organism such as an urchin) would imply a stronger selection pressure against increased size. However, if an increased probability of breakage represents an increased probability of dispersal, and if dispersal is sufficiently advantageous, there could be a selection pressure to increase the mean size of a population. Without further data concerning the survivorship and fecundity of broken blades, the role of mechanical factors in limiting the size of *M. complanata* remains questionable.

4. *An acorn barnacle, S. cariosus*.—An individual *S. cariosus* of the maximum size observed on Tatoosh Island has only $\approx 6\%$ greater chance of survival than an individual twice this size (Fig. 12d). For this species the mechanical factors discussed here clearly do not play an important role in size limitation.

5. *Limpets, C. digitalis, C. pelta, N. scutum*.—The survivorship curves for the three limpet species are shown in Fig. 13. The adhesive tenacity of stationary limpets of all three species is so great that mechanical limitation to size does not seem likely (Fig. 13a_{ii}, b_{ii}, c_{ii}). The decrease in tenacity accompanying locomotion, however, leads to another picture (Fig. 13a_i, b_i, c_i). In these cases Eq. 49 (which assumes randomly varying adhesive tenacity) has been used to calculate $P_{s,cum}$. Because the predicted rate of dislodgement of a population of moving snails is high, survivorship has been plotted against number of waves rather than months. For each of the three species, after relatively few waves individuals of the maximum observed size are at least eight times as likely to have survived as individuals of twice this size. For example, after 50 waves the survivorship ratio for *C. pelta* is 92 and for *N. scutum*, 455. After 150 waves it is 13 for *C. digitalis*. The survivorship ratios $L_r:2L_r$ and $L_r/2:L_r$ increase with the number of waves, the latter exceeding eight within the first 70 waves for *N. scutum* and *C. pelta* and within 350 waves for *C. digitalis*.

These survivorship data serve to emphasize the conclusion reached earlier, that for limpets there is a large risk associated with movement; the smaller the limpet the less this risk. Based on these approximate calculations, for at least the first 30–70 waves during a period of movement (150 to 350 waves for *C. digitalis*), the survivorship ratio is such that the mechanical constraints discussed here are likely to apply.

The survivorship curves suggest an approximate "critical value" for $L dP_d/dL$. The two species for which the ratio for survivorship to the end of a year is less than eight (*S. cariosus*, *M. californianus* end-on) have $L dP_d/dL$ values <0.10 at the maximum size observed in nature. In all cases where the survivorship ratio exceeds eight, $L dP_d/dL$ exceeds 0.10. It is on this basis

that we have chosen 0.10 as the cutoff value for designating LdP_d/dL as "large" or "small," but this value is intended only to serve as a "rule of thumb." Any rigorous definition of a critical value for LdP_d/dL above which size is limited by mechanical factors and below which size is limited by biological factors must take into account both the long-term flow regime at a particular site and the life history and demographics of the organism in question.

Our examples suggest that the approach used in this study may provide a useful tool for examining the size of solitary inflexible organisms exposed to flows of high velocity and high acceleration. In some cases consideration of mechanical factors alone may provide an adequate explanation for the observed size limits. In other cases mechanical factors are apparently of minor direct importance in size limitation, although an indirect affect (as in the case of the snails discussed above) is still possible. In these cases a search should be made for a biological limit to size, or alternatively for a mechanical mechanism setting an optimum size that is less than the maximum size possible.

Assumptions of the hypothesis

While this approach may be useful in many cases, we do not intend to imply that it can be applied to all wave-swept organisms, nor that it is a complete description of the forces those animals encounter. In particular, the model does not account for several aspects of the flow forces associated with waves, and several of the model's assumptions require further discussion.

1) The derived equations do not include a term for a moment tending to rotate an organism about an axis perpendicular to its basal plane, and thus torsional forces are ignored. Such torsional stresses would arise if F_{df} were to act along a line lying to one side of the center of adhesive area. It seems unlikely that this happens in organisms that are approximately radially symmetrical, such as limpets and barnacles, but the effect may be important for other species (e.g., certain corals) and in a truly general treatment must be taken into account.

2) The equations derived here assume that the flow forces experienced by an organism are not influenced by other organisms nearby, by surface rugosity, or by the presence of a boundary layer. These assumptions are probably valid for barnacles in the high intertidal zone and for limpets. However, the assumptions are clearly violated for other species in other habitats, mussels for example. The mussel tenacity measurements in this study were made on solitary mussels, which are occasionally found on Tatoosh Island, and thus are appropriate for our calculations. However, the vast majority of mussels on Pacific Northwest shores are not solitary, occurring instead in large, tightly packed beds (Paine and Levin 1981). Although hydrodynamic forces may be important in limiting the sizes of or-

ganisms in aggregations (see Mechanisms that Permit Wave-Swept Organisms to Attain Large Size, below), these forces are not appropriately described by our model.

3) The model assumes that the coefficients C_d , C_m , and C_l are constant for a given body shape. At least for C_d , the drag coefficient, this is a gross oversimplification; C_d clearly varies as a function of Reynolds number, Re , (Fig. 1) and, for a given set of flow parameters, is thus itself a function of size. The dependence of the inertia coefficient, C_m , and the lift coefficient, C_l , on Re is less clear, as is the dependence of all these coefficients on period parameter, K .

While insufficient data exist to precisely define the manner in which any size-dependent variation in C_d , C_m , and C_l affect the model, a general examination is possible. As the Reynolds number rises through the range 10^4 – 10^6 in steady state flow, C_d generally decreases gradually (Hoerner 1965, Vogel 1981). For example, the drag coefficient of a smooth sphere decreases from ≈ 0.47 to 0.10 as L_r increases from 0.005 m to 0.025 m in a steady flow velocity of 10 m/s (Hoerner 1965). However, if the surface of the object is rough or the shape less symmetrical, this effect is less pronounced. For example, for a cylinder with surface roughness elements of height only 1% of the diameter, C_d decreases only from 1.2 to ≈ 0.9 –1.0 in the Re range 10^4 – 10^6 . Further, as mentioned above, the drag coefficient of a plate-like shape decreases only slightly through a very large range of Re . For the most smooth and regularly shaped organisms dealt with here, limpets, C_d decreases only from ≈ 0.7 to 0.5 over a 10-fold increase in Re (10^4 to 10^5). Thus, while C_d is undoubtedly a function of size, its variation with size for these organisms is likely to be minimal. The variation of C_d with K has not been studied for biological objects. However, Sarpkaya and Tuter (1974) have shown that when Re is between 5×10^4 and 1×10^5 , the C_d of a cylinder is lower in harmonically oscillating flow than in steady flow. Thus, the C_d values used here probably overestimate the actual values at high Re .

The only relevant C_l vs. Re data available for objects near solid surfaces are those presented in Fig. 1. For the Re range measured, C_l appears to be independent of Re , and therefore of size. While these data are far too preliminary to draw any general conclusions, they do suggest that gross fluctuations in C_l in the Re range of interest are unlikely. The variation of C_l with K for biological objects is unknown.

The possibility of variation in C_m as a function of size is difficult to examine. In "ideal" (inviscid) flow, theory proclaims that C_m is a constant for a given shape, regardless of size (Batchelor 1967). We minimized the "nonideal" aspects of the flow by measuring C_m at very low velocities, and the measurements were close to those predicted by theory (Daniel 1982, 1983). The nature of the acceleration reaction in real, viscid

fluids is one of the current active areas of investigation in fluid dynamics. However, Sarpkaya and Tuter (1974) show, for spheres and cylinders, that for K greater than ≈ 20 (the range of interest here) C_m does not vary substantially. Sarpkaya and Tuter (1974) also show that C_m increases as Re increases from 10^4 to 10^6 . Verley and Moe (1979, cited in Sarpkaya and Isaacson 1981) show that C_m for a cylinder is virtually constant at all K 's when a fast unidirectional current is superimposed on a harmonically oscillating flow. This flow regime is similar to that encountered in a turbulent bore. If these results hold true for biological objects near a solid boundary it is quite possible that the C_m values are higher than those used in our calculations. Further research will be necessary to evaluate this possibility.

We speculate, then, that full knowledge of the variation in C_d , C_b , and C_m would reveal the C_d values used here to be overestimates, the C_i values approximately correct, and the C_m values underestimates. The result of correcting the model for the size-dependent variation in coefficients would be to: (1) lower the estimate of the size-independent probability of dislodgement and (2) increase the calculated value of $L dP_d/dL$. Thus, if our speculation about the size-dependence of C_d , C_m , and C_i is correct, our argument for the role of water acceleration in size limitation would be strengthened by the inclusion of variable coefficients.

4) The calculation of $L dP_d/dL$ depends in part on the distribution of breaking stresses present in a population. This distribution was estimated using actual breaking stress measurements, which themselves contained some experimental error. Unless these experimental errors were strongly biased (e.g., if the basal area of small barnacles was overestimated while that of large barnacles was underestimated), they increased the apparent variance of the breaking stress distribution; all reasonable precautions were taken to preclude such biases. From an examination of Eqs. 40 and 41 it can be seen that an increase in variance decreases the calculated $L dP_d/dL$. Thus, any future improvement in measuring technique, by giving a better estimate of the true breaking stress distribution will, by decreasing the variance, increase the estimate of $L dP_d/dL$ for a species and thereby strengthen our argument for the role of acceleration in size limitation.

5) The model assumes that adhesive tenacity is independent of the rate at which a dislodging force is applied. This need not be the case, and in general the strength of biological materials increases as the rate at which they are deformed increases (Wainwright et al. 1976). However, the only data concerning this point available for wave-swept organisms are those of Grenon and Walker (1982), who showed that the adhesive tenacity of the limpet *Patella vulgata* decreases as the dislodging deformation is applied faster. Further research is necessary before the full effect on this analysis of the rate of deformation can be known.

Mechanisms that permit wave-swept organisms to attain large size

Our predictions of mechanical limits to size of wave-swept organisms have been made for solitary, rigid animals. However, a number of plants and animals on surf-beaten shores have features that permit them to attain sizes larger than our model would predict. Possible mechanisms permitting large size include: strengthening the basal adhesive, aggregation, posturing, flexibility, pruning, and reproduction before seasonal or rare large waves hit.

Before exploring these mechanisms permitting large size, we should ask whether the largest wave-swept organisms (seaweeds and corals) simply use a stronger basal adhesive and are made of stronger material (i.e., have a higher σ_{max}) than their smaller neighbors. Values for σ_{max} for various seaweeds (Delf 1932, Koehl and Wainwright 1977, Koehl 1979), and corals (Table 1; see also Wainwright et al. 1976, Vosburgh 1977, 1982, Chamberlain 1978) are similar to or below the σ_{max} values reported here for smaller organisms. Furthermore, once the adhesive strength of the organism exceeds that of the rock or other organisms to which it is stuck, the organism cannot effectively increase its ability to stay attached to the shore by a further increase in strength. In many cases when we were dislodging plants or animals, the rock to which the organisms were attached failed before the organism came unstuck. For example, of 351 *B. glandula* dislodged at Mukkaw Bay, 47% came off because the rock, rather than the barnacle, failed.

As mentioned above (Assumptions of the Hypothesis), many intertidal organisms occur in dense aggregations. Monospecific stands may be due to asexual reproduction (e.g., clonal sea anemones, *Anthopleura elegantissima*) or to patterns of settlement, growth, and survival (e.g., stalked barnacles, *Pollicipes polymerus*, mussels, *M. californianus*, seaweeds, *P. palmaeformis*). Furthermore, on many wave-swept shores, space is a limited resource (Connell 1961b, 1978, Paine 1966, Dayton 1971, Quinn 1979, Paine and Levin 1981) and on such sites the organism surrounded by bare substratum rather than a host of other organisms is rare indeed. Organisms in aggregations, shielded by their neighbors, are exposed to much lower flow velocities and accelerations than those characterizing mainstream flow at a site (Wainwright and Koehl 1976, Koehl 1977a, b). The water flow within mussel beds, even on exposed coasts, can be so slow that sediment accumulates and delicate organisms can live there (Connell 1972, Suchanek 1979).

At least in some cases, hydrodynamic forces are important in removing aggregated organisms from the shore, large organisms or clumps being more susceptible than small ones to being blown away (Harger and Landenberger 1971, Connell 1972, Paine and Levin

1981). For our model to be useful in predicting the probability of washing away of gregarious animals or plants, flow and tenacity measurements for organisms within a clump are required. For some organisms (e.g., *Pollicipes polymerus*), a more useful approach might be to apply the model to the entire clump rather than to individuals within it.

If an organism on a crowded shore is bigger than its neighbors, it can stick out into much faster flow (e.g., Wainwright and Koehl 1976). In such a situation, the difference in magnitude between the mechanical stresses experienced by the large and small organisms would be even greater than predicted by our model, which assumes that the flows encountered by large and small creatures are the same.

Some animals can actively change their body shape or orientation in response to water flow. For example, the surge-channel sea anemones *Anthopleura xanthogrammica* can actively adjust their height so that they do not protrude above their neighbors, and can assume a pancake-like posture (thereby minimizing C_m and C_d) when in rapid flow (Koehl 1977a). Mobile animals, such as snails, can move into protected microhabitats on wave-beaten shores.

Asymmetric animals such as mussels may grow with their long axis oriented in the direction of flow, thus reducing the added mass coefficient. Orientation is only useful when flow direction is predominantly along one axis, such as in surge channels. Observations on Tatoosh suggest that mussels are, in fact, oriented with their long axis parallel to flow in surge channels.

Flexible organisms such as seaweeds can attain relatively large size on wave-swept shores. For example, macroalgae such as *Lessoniopsis littoralis* in the low intertidal zone on Tatoosh Island can reach lengths (stipe plus blades) > 1 m (see Abbott and Hollenberger 1976). Flexibility can decrease the hydrodynamic forces organisms must resist, and hence can make larger bodies mechanically possible, by several mechanisms. (1) Tall, flexible organisms tend to be bent over by moving water so that their long axes are parallel to the flow. Furthermore, the branches or lobes of flexible organisms may be stacked or folded by moving water into more compact shapes with lower drag coefficients (C_d) (Fraser 1962, Charters et al. 1969, Koehl 1977a, Vogel 1984). Since the drag force on an organism depends on its projected area normal to the flow (A_p) and on its C_d (Eq. 17), the drag on a flexible organism can be lower than on a rigid organism of the same size and original shape. The bending over or deforming of flexible organisms in waves can also reduce the acceleration reaction force (Eq. 19); the C_m 's of flattened bodies parallel to the direction of acceleration are lower than those of spherical bodies, which in turn are lower than the C_m 's of flattened bodies normal to the direction of acceleration (Daniel 1983). Furthermore, if a tall flexible organism is surrounded by other organisms or is thin (very flat or narrow) compared with the boundary

layer (δ ; Eq. 16) along the substratum, it can be bent over by moving water into a position closer to the substratum, where it encounters slower flow. (2) Flexible organisms that are long enough can avoid bearing hydrodynamic forces at times during a wave when they are likely to be greatest (i.e., when dU/dt and U are highest; Eqs. 19 and 17). For example, a very floppy, long alga such as *Durvillea antarctica* moves with the water in a wave as it rushes up the shore; the thallus of the plant is not substantially stretched until the alga is strung out in the direction of flow and is no longer free to move with the water. If such a flexible organism is long enough, the water may be slowing down or have reversed direction before the slack in the plant can be taken up. Thus, for long, floppy organisms in oscillating flow, an increase in length can lead to a decrease in the forces the organism has to bear. (3) Deformable organisms are good "shock absorbers." A hydrodynamic force on such an organism bends or stretches the body, and not until the body is fully deformed is the entire load transmitted to the area of attachment to the substratum. Thus, high forces of short duration (such as occur on organisms in waves) can be damped out by bendable, soft, or stretchable bodies (Pain 1968, Thomson 1981).

That flexibility can be an effective mechanism for withstanding wave action was clearly illustrated when Hurricane Allen hit the Jamaican coral reefs in 1980; rigid, brittle organisms such as stony corals suffered more breakage than did flexible, deformable organisms like gorgonians (Woodley et al. 1981). On the other hand, in certain cases flexibility may reduce the likelihood that an organism will survive in a wave-beaten habitat. If a flexible organism flaps (like a flag) in the flow, it can experience higher drag than a rigid structure of the same size and shape (Hoerner 1965). Furthermore, if structures are flexible enough to oscillate in waves, they can perish by fatigue fracture (Wiegel 1972). The behavior of flexible organisms in waves is a complex mechanical problem that merits further analysis.

Some sessile organisms (e.g., certain algae and colonial invertebrates) achieve larger size during non-stormy intervals than they can maintain during storms; organisms are pruned to smaller sizes during periods of heavy wave action rather than being completely ripped off the substratum. The heaviest wave action generally accompanies seasonal storms (Schwenke 1971, Harger 1972, Menge 1972, Paine and Levin 1981) or isolated events like hurricanes and typhoons (Stoddart 1962, 1963, Endean 1976, Randall and Eldredge 1977, Smith and Harrison 1977, Vosburgh 1977, Woodley et al. 1981, Highsmith 1982). The places where pieces of the organism break off may be determined by the construction of the organism itself (e.g., Highsmith 1982) or by the activities of grazers on and bioeroders of the organism (e.g., Black 1976, Santelices et al. 1980, Highsmith 1982). The "stump" that is left behind after such pruning can continue to live and may grow to

large size again during subsequent intervals of calm water. In some cases, not only does the stump survive, but so do broken-off fragments. "Programmed fragmentation" of this sort has been proposed as a mechanism of asexual reproduction and dispersal for many corals (Chamberlain 1978, Tunnicliffe 1980, 1981, Highsmith 1982).

In habitats where large waves occur only seasonally or during rare storms, organisms that grow rapidly during calm intervals can become too large to survive the next onslaught of violent water movement. However, if such organisms can produce gametes or spores before they are blown away, and if their propagules can recolonize the habitat, then selection for smaller size by wave-induced mortality should not be strong. An example of such a rapidly growing, early reproducing large organism that thrives on exposed shores that have predictable seasonal periods of heavy wave action is the seaweed *Durvillea antarctica* (Santelices et al. 1980).

To this point we have dealt solely with mechanical limits to size, and have treated large size as if it were always advantageous to the organism. This is not necessarily so, and in order to establish a useful context for the examination of real wave-swept communities, we briefly discuss the biological advantages and disadvantages of size.

Is big good?

Large size may be advantageous to an organism by increasing its persistence on the shore, by increasing its reproductive output, or both. These results may be achieved through a number of specific advantages.

Large individuals are better able than small individuals to ward off some types of predators (Gould 1966, Connell 1970, Stanley 1973, Zaret and Kerfoot 1975). A number of cases of benthic organisms escaping in size from predation have been documented (Ansell 1960, Paine 1965, 1976a, Dayton 1971, Palmer 1979; a number of other studies have been reviewed by Connell 1972 and by Vermeij 1978). Furthermore, in some cases inferior competitors can escape in size from being overgrown by members of other species (Sebens 1980). Tall solitary organisms are often less susceptible than smaller ones to being overgrown by encrusting colonial animals (Jackson 1977).

Because large organisms have a lower ratio of surface area to volume than do smaller creatures, a large organism is better insulated from fluctuations in external conditions and can regulate internal environment more easily (Gould 1966, Stanley 1973). Many organisms exposed to wave action are intertidal and thus are often also exposed to drying in air and/or heating in the sun. Large intertidal organisms often survive exposure to air longer than do smaller members of the same species (e.g., Johnson and Shick 1977). Although a sessile individual must survive while small in the same spot as when large (Paine 1981), daytime low spring tides during warm sunny weather are seasonal occurrences at

many sites; an organism settling at such a site could conceivably grow beyond desiccation-vulnerable small size before the harsh tides occur.

Large organisms may have a greater likelihood of surviving damage than small ones. Plants and animals on wave-beaten shores are sometimes bashed by waterborne projectiles such as logs (Dayton 1971) or coral rubble (Endean 1976, Randall and Eldredge 1977, Highsmith et al. 1980). Although large corals are more likely than small ones to suffer some damage by projectiles (Woodley et al. 1981), large corals are less likely than small ones to be detached or destroyed when hit by a projectile (Highsmith 1981, Woodley et al. 1981). Furthermore, large pieces of coral that are broken off have a greater chance of surviving than do small ones (Highsmith 1980, 1982, Highsmith et al. 1980). On the other hand, of course, if an animal is small enough to live in a crevice, its probability of being scraped off the substratum by a projectile is very low (Connell 1972, Paine 1981).

As mentioned previously, size may directly affect reproductive output. Large animals have more "room" (volume) in their bodies in which gonadal tissue might develop (Sebens 1982). Gould (1966) has suggested that large invertebrates can have more progeny per brood than small ones, and Menge (1974) has demonstrated that the fecundity of large *Leptasterias* (starfish) is greater than that of small ones. This relationship is quite general among invertebrates; for a review see Giese and Pearse (1974).

Another advantage of increasing body size is that new categories of food can become available to an organism if it becomes big enough (e.g., Gould 1966, Stanley 1973, Wilson 1975). Examples of wave-swept organisms that can, once they attain a large size, capture and ingest new types of food are provided by Menge (1972) and Sebens (1979, 1981, 1982).

Large organisms are more efficient metabolically (i.e., have a lower metabolic rate per unit body mass) than small organisms (Gould 1966, Schmidt-Nielsen 1974). Furthermore, big mussels can achieve their maximum growth rate on a lower relative food ration than can small ones (Griffiths and King 1979).

Biological factors limiting the size of wave-swept organisms

In spite of the many benefits of being big, a number of biological factors can counteract the selective advantage of large size or can locally prevent individuals from attaining the maximum size that is both biologically and mechanically possible for their species. For example, some snail and starfish predators have been found to preferentially eat large rather than small individuals of some barnacle species (Connell 1961a, 1971, Paine 1966, 1981, Palmer 1980), and may thus remove the big individuals from a population. If a particular type of organism must hide (from desiccation, waves, or predators, for example), the sizes of

refuges available at a particular site may limit its maximum size (Kohn 1971, Emson and Faller-Fritsch 1976, Paine 1981); organisms too big to fit into the refuges perish. The allocation of resources to the repair of wave-inflicted damage rather than to growth may also limit the size of wave-beaten creatures (Ebert 1968).

The size, and therefore the reproductive output, an organism attains also depends in part upon the quantity and quality of food available to it in a particular habitat relative to its metabolic demands (e.g., sea anemones: Sebens 1982; gastropods: Frank 1965, Paine 1965, 1969, Sutherland 1970; bivalves: Stanley 1973, Griffiths and King 1979; starfish: Smith 1940, Paine 1976*a*; sea urchins: Ebert 1968, Vadas 1977; fish: Kerr 1971). Many intertidal animals may have to stop feeding when exposed to air or when wave action is severe, and thus may spend a smaller fraction of each day eating than subtidal animals. Reduced feeding time, in combination, in some cases, with lower food availability or increased metabolic rate (due to warming up when out of the water), have been cited as responsible for the observed trend that high intertidal animals are smaller than low intertidal ones (Connell 1961*a*, 1972, Seed 1969, Sutherland 1970, Dayton 1971, Vermeij 1972, 1978, Paine 1974, Suchanek 1979, Sebens 1980). This pattern of size distribution has also been ascribed to the migration of larger animals to lower positions on the shore (Paine 1969, Bertness 1977). However, a few intertidal species show the opposite trend in size distribution, with larger individuals higher on the shore (Frank 1965). Various special mechanisms responsible for these exceptions are listed by Vermeij (1978).

Although large animals have a lower metabolic rate per unit mass than small ones, their total metabolic rate per individual is greater. If the metabolic rate of an animal increases as a greater power of body mass than does the rate at which an animal can take in energy, the scope for growth (*sensu* Sebens 1979) rises to some maximum and then decreases as body size increases (e.g., mussels: Vahl 1973, Thompson and Bayne 1974, Griffiths and King 1979; cnidarians: Sebens 1979, 1981, 1982). For such organisms an upper size limit exists at the point where scope for growth equals zero. Sebens (1979, 1981) suggests that such organisms should get no larger than the "optimal size" at which scope for growth, and hence gonad production, is maximized. This optimal size is smaller than the maximal size, and is a function of habitat quality.

Applications of the model of size-dependent mechanical failure

In light of these many concurrently operating factors affecting body sizes in a population, how can our model be usefully applied?

Our analysis provides a quantitative method for deciding whether wave forces alone can limit the size of a particular species at a particular site. From the estimated or measured values for the parameters of the

model, the probability of dislodgement and the size-specific increment in probability of dislodgement can be calculated. Coupled with information about the life history of the species and the flow regime at that site, a survivorship ratio can be estimated. If this ratio is greater than eight, it is possible that the size of the species is limited at that site by the wave forces encountered, and further experimental efforts may be made to investigate this possibility. In such a case an examination solely of the possible biological factors limiting size would be ill-advised. Inversely, if the survivorship ratio is substantially lower than eight, wave forces may reasonably be discounted and further efforts focused on the role of biological interactions.

Even in cases where wave forces are deemed to be only marginally involved in determining the upper size limit, a consideration of these forces may prove useful in examining the optimal (as opposed to the maximal) size that a species attains. Size-specific mortality due to wave forces could conceivably serve to decrease the size at which an organism optimizes its intrinsic rate of increase (*sensu* Roff 1981) and could thereby affect size selection.

Alexander (1981) has outlined a theory for predicting the safety factors with which biological structures are constructed. Data collected for assessing optimal size may also be used to predict optimal safety factors.

The methods outlined here may prove useful in examining the morphological diversity of organisms. Vermeij (1978) has suggested that the greater diversity of snail shell types found in protected as compared with exposed habitats is due to the limits on shell form imposed by wave action. Similarly, we might expect to find a greater diversity of form among small than among large organisms on wave-swept shores. Stanley (1973), Bonner and Horn (1982), and Horn et al. (1982) have mentioned various other physical constraints on form that affect the morphological diversity of large, but not small, organisms. These propositions can now be quantitatively tested.

Our model, by quantifying the "exposure" (probability of dislodgement) of organisms, may prove useful in several aspects of behavioral and community ecology. Because wave action can limit the time a motile organism can forage without being in danger of washing away (e.g., Menge 1972), and because large animals (both predators and prey) are more likely to be washed away than small ones, the foraging strategies of large vs. small animals on protected vs. exposed shores might be expected to be different. The role of disturbance in maintaining the diversity of communities has been discussed by a number of authors (Levin and Paine 1974, 1975, Connell and Slayter 1977, Connell 1978, Quinn 1979, Sousa 1979*a, b*, Paine and Levin 1981). Waves, which are an important agent of disturbance on many rocky shores and coral reefs, are more likely to remove large than small organisms from the substratum. Such differential susceptibility of organisms to disturbance

may have important consequences for the age structure and species composition of wave-swept communities. Furthermore, the time required for the particular primary space-holders in a community to grow to wave-vulnerable size, coupled with the temporal pattern of heavy wave action at a site, should be of basic importance in the dynamics of the community (Paine and Levin 1981).

Size-dependent predation can have important effects on population and community structure (Brooks and Dodson 1965, Galbraith 1967, Zaret and Kerfoot 1975). Wave action that selectively removes large individuals from a population should have similar effects. Note that the more exposed a habitat, the smaller the size at which it is highly probable that a particular type of organism will be washed away.

Sessile organisms often provide a habitat in which other organisms live. Often the larger the sessile organisms, the greater the diversity of the community of organisms living amongst them (MacArthur and MacArthur 1961, Smith 1972, Paine 1976a, Suchanek 1979). Thus, the sizes at which sessile organisms are likely to wash away in habitats of different wave exposure should have important effects on overall community structure.

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LITERATURE CITED

- Abbott, I. A., and G. J. Hollenberger. 1976. Marine algae of California. Stanford University Press, Stanford, California, USA.
- Adey, W. H. 1978. Coral reef morphogenesis: A multidimensional model. *Science* **202**:831-837.
- Alexander, R. McN. 1968. Animal mechanics. University of Washington Press, Seattle, Washington, USA.
- . 1971. Size and shape. Edward Arnold, London, England.
- . 1981. Factors of safety in the structure of animals. *Science Progress* **67**:109-130.
- Ansell, A. D. 1960. Observations on predation of *Venus striatula* (da Costa) by *Natica alderi* Forbes. *Proceedings of the Malacological Society of London* **34**:157-164.
- Banse, K., and S. Mosher. 1980. Adult body mass and annual production/biomass relationships for field populations. *Ecological Monographs* **50**:355-379.
- Batchelor, G. K. 1967. An introduction to fluid mechanics. Cambridge University Press, London, England.
- Bertness, M. D. 1977. Behavioral and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*. *Ecology* **58**:86-97.
- Black, R. 1976. The effects of grazing by the limpet, *Acmaea insessa*, on the kelp *Egregia laevigata*. *Ecology* **57**:265-277.
- Bonner, J. T. 1968. Size change in development and evolution. Pages 1-15 in D. B. Macurda, editor. Paleobiological aspects of growth and development. Paleontological Society Memoir **2**.
- Bonner, J. T., and H. S. Horn. 1982. Selection for size, shape, and developmental timing. Pages 259-276 in J. T. Bonner, editor. Evolution and development. Dalmhor Konferenzen 1982. Springer-Verlag, New York, New York, USA.
- Branch, G. M., and A. C. Marsh. 1978. Tenacity and shell shape in six *Patella* species: adaptive features. *Journal of Experimental Marine Biology and Ecology* **34**:111-130.
- Brooks, J. L., and S. J. Dodson. 1965. Predation, body size, and composition of plankton. *Science* **150**:28-35.
- Carstens, T. 1968. Wave forces on boundaries and submerged bodies. *Sarsia* **34**:37-60.
- Chamberlain, J. A., Jr. 1978. Mechanical properties of coral skeleton: compressive strength and its adaptive significance. *Paleobiology* **4**:410-435.
- Charters, A. C., M. Neushul, and C. Barilotti. 1969. The functional morphology of *Eisenia arborea*. *Proceedings of the International Seaweed Symposium* **6**:89-105.
- Cokelet, E. D. 1977. Breaking waves. *Nature (London)* **267**:769-774.
- . 1979. Breaking waves—the plunging jet and interior flow field. Pages 288-301 in T. L. Shaw, editor. Mechanics of wave-induced forces on cylinders. Pittman Advanced Publishing Program, San Francisco, California, USA.
- Connell, J. H. 1961a. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**:710-723.
- . 1961b. Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacles, *Balanus balanoides*. *Ecological Monographs* **31**:101-104.
- . 1970. A predatory-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs* **40**:44-78.
- . 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations*, Oosterbeek, 1970. Centre for Agricultural Publishing and Documentation (PUDOC), Wageningen, The Netherlands.
- . 1972. Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* **3**:169-192.
- . 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**:1303-1310.
- Connell, J. H., and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Currey, J. 1970. Animal skeletons. Edward Arnold, London, England.
- Daniel, T. L. 1982. The role of added mass in locomotion with special reference to medusae. Dissertation. Duke University, Durham, North Carolina, USA.
- . 1983. Mechanics and energetics of medusan jet propulsion. *Canadian Journal of Zoology* **61**:1406-1420.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization

- zation of space in a rocky intertidal community. *Ecological Monographs* **41**:351-389.
- . 1973. Two causes of resource partitioning in an intertidal community: making the right prediction for the wrong reason. *American Naturalist* **107**:662-670.
- Delf, E. M. 1932. Experiments with the stipes of *Fucus* and *Laminaria*. *Journal of Experimental Biology* **9**:300-313.
- Denny, M. W. 1982. Forces on intertidal organisms due to breaking waves: design and application of a telemetry system. *Limnology and Oceanography* **27**:178-183.
- Ebert, T. A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology* **49**:1075-1093.
- Emsom, R. H., and R. J. Faller-Fritsch. 1976. An experimental investigation into the effect of crevice availability on abundance and size structure in a population of *Littorina rudis* (Maton): Gastropoda: Prosobranchia. *Journal of Experimental Marine Biology and Ecology* **23**:285-297.
- Endean, R. 1976. Destruction and recovery of coral reef communities. Pages 215-254 in O. A. Jones and R. Endean, editors. *Biology and geology of coral reefs*. Volume 3, *Biology II*. Academic Press, New York, New York, USA.
- Frank, P. W. 1965. The biodemography of an intertidal snail population. *Ecology* **46**:831-844.
- Fraser, A. I. 1962. Wind tunnel studies of the forces acting on the crowns of small trees. Pages 178-183 in Report on Forest Research. Her Majesty's Stationery Office, London, England.
- Frost, B. W. 1980. The inadequacy of body size as an indicator of niches in the zooplankton. Pages 742-753 in W. C. Kerfoot, editor. *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, New Hampshire, USA.
- Galbraith, M. G., Jr. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. *Transactions of the American Fisheries Society* **96**:1-10.
- Galilei, G. 1638. *Discorsie e dimostrazioni matematiche, intorno due nuove scienze . . .* [Dialogues concerning two new sciences]. Translated by H. Crew and A. de Salvio. 1914, reprinted 1950. Northwestern University Press, Evanston, Illinois, USA.
- Galvin, C. J. 1972. Wave breaking in shallow water. Pages 413-456 in R. E. Meyer, editor. *Waves on beaches and resulting sediment transport*. Academic Press, New York, New York, USA.
- Giese, A. C., and J. S. Pearse. 1974. *Reproduction of marine invertebrates*. Academic Press, New York, New York, USA.
- Glynn, P. W. 1973. Aspects of the ecology of coral reefs in the Western Atlantic region. Pages 271-324 in O. A. Jones and R. Endean, editors. *Biology and geology of coral reefs*. Volume 2, *Biology I*. Academic Press, New York, New York, USA.
- Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews* **41**:587-640.
- Grassle, J. F. 1973. Variety in coral reef communities. Pages 247-270 in O. A. Jones and R. Endean, editors. *Biology and geology of coral reefs*. Volume 2, *Biology I*. Academic Press, New York, New York, USA.
- Graus, R. R., J. A. Chamberlain, and A. M. Boker. 1977. Structural modifications of corals in relation to waves and currents. *Studies in Geology* **4**:135-153.
- Gray, B. F. 1981. On the "surface law" and basal metabolic rate. *Journal of Theoretical Biology* **93**:757-767.
- Grenon, J.-F., and G. Walker. 1982. The tenacity of the limpet *Patella vulgata* L.: an experimental approach. *Journal of Experimental Marine Biology and Ecology* **54**:277-308.
- Griffiths, C. L., and J. A. King. 1979. Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. *Marine Biology (Berlin)* **51**:141-149.
- Haldane, J. B. S. 1928. On being the right sizes. Pages 20-28 in J. B. S. Haldane. *Possible worlds and other papers*. Harper, New York, New York, USA.
- Harger, J. R. E. 1970. The effect of wave impact on some aspects of the biology of sea mussels. *Veliger* **12**:401-414.
- . 1972. Competitive co-existence: Maintenance of interacting associations of the sea mussels *Mytilus edulis* and *Mytilus californianus*. *Veliger* **14**:387-410.
- Harger, J. R. E., and D. E. Landenberger. 1971. The effect of storms as a density dependent mortality factor on populations of sea mussels. *Veliger* **14**:195-201.
- Highsmith, R. C. 1980. Passive colonization and asexual colony multiplication in the massive coral *Porites lutea* Milne Edwards. *Journal of Experimental Marine Biology and Ecology* **47**:55-67.
- . 1981. Coral bioerosion at Enewetak: Agents and dynamics. *Internationale Revue der Gesamten Hydrobiologie* **66**:335-375.
- . 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series* **7**:207-226.
- Highsmith, R. C., A. C. Riggs, and C. M. D'Antonio. 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia* **46**:322-329.
- Hoerner, S. F. 1965. *Fluid-dynamic drag*. Hoerner Press, Brick Town, New Jersey, USA.
- Hoerner, S. F., and H. V. Borst. 1975. *Fluid-dynamic lift*. Hoerner Press, Brick Town, New Jersey, USA.
- Horn, H. S., J. T. Bonner, W. Dohle, M. J. Katz, M. A. R. Koehl, H. Meinhardt, R. A. Raff, W.-E. Reif, S. C. Stearns, and R. Strathmann. 1982. Adaptive aspects of development. Pages 215-235 in J. T. Bonner, editor. *Evolution and development*. Dahlem Konferenzen 1982. Springer-Verlag, New York, New York, USA.
- Hutchinson, G. E. 1971. Scale effects in ecology. Pages xvii-xxvi in G. C. Patil, E. P. Pielou, and W. E. Waters, editors. *Statistical ecology*, Volume 1. Pennsylvania State University Press, University Park, Pennsylvania, USA.
- Hutchinson, G. E., and R. H. MacArthur. 1960. A theoretical ecological modal of size distributions among species of animals. *American Naturalist* **93**:117-125.
- Jackson, J. B. C. 1977. Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *American Naturalist* **111**:743-767.
- Johnson, L. L., and J. M. Shick. 1977. Effects of fluctuating temperature and immersion on asexual reproduction in the intertidal sea anemone *Haliplanella luciae* (Berill) in laboratory culture. *Journal of Experimental Marine Biology and Ecology* **28**:141-149.
- Jones, W. E., and A. Demetropoulos. 1968. Exposure to wave action; measurements of an important ecological parameter on the shores of Anglesey. *Journal of Experimental Marine Biology and Ecology* **2**:46-63.
- Keller, H. B., D. A. Levine, and G. B. Whitham. 1960. Motion of a bore over a sloping beach. *Journal of Fluid Mechanics* **7**:302-316.
- Kerr, S. P. 1971. Prediction of fish growth efficiency in nature. *Journal of the Fisheries Research Board of Canada* **28**:809-814.
- . 1974. Theory of size distributions in ecological communities. *Journal of the Fisheries Research Board of Canada* **31**:1859-1862.
- Keulegan, G. H., and L. H. Carpenter. 1958. Forces on cylinders and plates in an oscillating fluid. *Journal of Research of the National Bureau of Standards* **60**:423-440.
- Kinsman, B. 1965. *Wind waves*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

- Koehl, M. A. R. 1977a. Effects of sea anemones on the flow forces they encounter. *Journal of Experimental Biology* **69**: 127-142.
- . 1977b. Water flow and the morphology of zoanthid colonies. Pages 437-444 in *Proceedings of the Third International Coral Reef Symposium*. Volume 1, Biology. Rosentiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA.
- . 1979. Stiffness or extensibility of intertidal algae: A comparative study of modes of withstanding wave action. *Journal of Biomechanics* **12**:634.
- Koehl, M. A. R., and S. A. Wainwright. 1977. Mechanical adaptations of a giant kelp. *Limnology and Oceanography* **22**:1067-1071.
- Kohn, A. J. 1971. Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. *Limnology and Oceanography* **16**:332-348.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences (USA)* **71**:2744-2747.
- Levin, S. A., and R. T. Paine. 1975. The role of disturbance in models of community structure. Pages 56-67 in S. A. Levin, editor. *Ecosystem analysis and prediction*. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.
- Lewis, J. P. 1968. Water movements and their role in rocky shore ecology. *Sarsia* **34**:13-36.
- Longuet-Higgins, M. S. 1982. Parametric solutions for breaking waves. *Journal of Fluid Mechanics* **121**:403-424.
- Longuet-Higgins, M. S., and J. S. Turner. 1974. An 'entraining plume' model of a spilling breaker. *Journal of Fluid Mechanics* **63**:1-20.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* **42**:594-598.
- Maynard-Smith, J. 1968. *Mathematical ideas in biology*. Cambridge University Press, Cambridge, England.
- McMahon, T. 1973. Size and shape in biology. *Science* **179**: 1201-1204.
- . 1975. The mechanical design of trees. *Scientific American* **233**:93-102.
- . 1980. Scaling physiological time. *Lectures in mathematics in the life sciences* **13**:131-163.
- Menge, B. A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecological Monographs* **42**:25-50.
- . 1974. Effect of wave action and competition on brooding and reproductive effort in the seastar *Leptasterias hexactis*. *Ecology* **55**:84-93.
- Miller, S. L. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. *Journal of Experimental Marine Biology and Ecology* **14**:99-156.
- Pain, H. J. 1968. *The physics of vibrations and waves*. John Wiley and Sons, New York, New York, USA.
- Paine, R. T. 1965. Natural history, limiting factors and energetics of the opisthobranch *Navanax inermis*. *Ecology* **46**:603-619.
- . 1966. Food web complexity and species diversity. *American Naturalist* **100**:65-75.
- . 1969. The *Pisaster-Tegula* interaction: Prey patches, predator food preference and intertidal community structure. *Ecology* **50**:950-961.
- . 1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)* **15**:93-120.
- . 1976a. Size-limited predation: An observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* **57**:858-873.
- . 1976b. Biological observations on a subtidal *Mytilus californianus* bed. *Veliger* **19**:125-130.
- . 1981. Barnacle ecology: Is competition important? The forgotten roles of disturbance and predation. *Paleobiology* **7**:553-560.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* **51**:145-178.
- Palmer, A. R. 1979. Fish predation and the evolution of gastropod shell sculpture: Experimental and geographic evidence. *Evolution* **33**:697-713.
- . 1980. A comparative and experimental study of feeding and growth in Thaidid gastropods. Dissertation. University of Washington, Seattle, Washington, USA.
- Pedley, T. J., editor. 1977. *Scale effects in animal locomotion*. Academic Press, New York, New York, USA.
- Peregrine, D. H. 1972. Equations for water waves and the approximations behind them. Pages 95-121 in R. E. Meyer, editor. *Waves on beaches and resulting sediment transport*. Academic Press, New York, New York, USA.
- . 1983, *in press*. Breaking waves on beaches. *Annual Review of Fluid Mechanics*.
- Platt, T., and W. Silvert. 1981. Ecology, physiology, allometry, and dimensionality. *Journal of Theoretical Biology* **93**:855-860.
- Quinn, J. F. 1979. Disturbance, predation and diversity in the rocky intertidal zone. Dissertation. University of Washington, Seattle, Washington, USA.
- Randall, R. H., and L. G. Eldredge. 1977. Effects of typhoon Pamela on the coral reefs of Guam. Pages 525-531 in *Proceedings of the Third International Coral Reef Symposium*. Volume 2, Geology. Rosentiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA.
- Riedl, R. 1971. Water movement: Animals. Pages 1123-1156 in O. Kinne, editor. *Marine ecology*, Volume 1, Part 2. Wiley-Interscience, New York, New York, USA.
- Roff, D. A. 1981. On being the right size. *American Naturalist* **118**:405-422.
- Santelices, B., J. C. Castilla, J. Cancino, and P. Schmiede. 1980. Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in central Chile. *Marine Biology (Berlin)* **59**:119-132.
- Sarpkaya, T., and M. Isaacson. 1981. *Mechanics of wave forces on offshore structures*. Van Nostrand Reinhold, New York, New York, USA.
- Sarpkaya, T., and O. Tuter. 1974. Forces on cylinders and spheres in a sinusoidally oscillating fluid. Technical Report NPS-595674091, Naval Postgraduate School, Monterey, California, USA.
- Schlichting, H. 1979. *Boundary layer theory*. Seventh edition. McGraw-Hill, New York, New York, USA.
- Schmidt-Nielsen, K. 1974. Scaling in biology: The consequences of size. *Experimental Zoology* **194**:287-308.
- Schwenke, H. 1971. Water movement: Plants. Pages 1092-1121 in O. Kinne, editor. *Marine ecology*, Volume 1, Part 2. Wiley-Interscience, New York, New York, USA.
- Sebens, K. P. 1979. The energetics of asexual reproduction and colony formations in benthic marine invertebrates. *American Zoologist* **19**:683-697.
- . 1980. The control of asexual reproduction and indeterminate body size in the sea anemone *Anthopleura elegantissima* (Brandt). *Biological Bulletin* **158**:370-382.
- . 1981. The allometry of feeding, energetics, and body size on three sea anemone species. *Biological Bulletin* **161**: 152-171.
- . 1982. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology* **63**:209-222.

- Seed, R. 1969. The ecology of *Mytilus edulis* (Lamallibranchiata) on exposed rocky shores II. Growth and mortality. *Oecologia* (Berlin) 3:317-350.
- Silvert, W., and T. Platt. 1981. Dynamic energy-flow model of particle-size distribution in pelagic ecosystems. Pages 754-763 in W. C. Kerfoot, editor. *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, New Hampshire, USA.
- Smith, F. E. 1972. Spatial heterogeneity, stability and diversity in ecosystems. *Transactions Connecticut Academy of Arts and Sciences* 44:309-335.
- Smith, G. F. M. 1940. Factors limiting distribution and size in the starfish. *Journal of the Fisheries Research Board of Canada* 5:84-103.
- Smith, S. V., and J. T. Harrison. 1977. Calcium carbonate production of the *mare incognitum*, the upper windward reef slope, at Enewetak Atoll. *Science* 197:556-559.
- Sousa, W. P. 1979a. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49:227-254.
- . 1979b. Disturbances in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225-1239.
- Stanley, S. M. 1973. An explanation for Cope's rule. *Evolution* 27:1-26.
- Stive, M. J. F. *In press*. Velocity and pressure field of spilling breakers. *Proceedings of the 17th International Conference on Coastal Engineering*, March 23-28, 1980, Sydney, Australia. American Society of Mechanical Engineers, New York, New York, USA.
- Stoddart, D. R. 1962. Catastrophic storm effects on the British Honduras reefs and cays. *Nature* 196:512-515.
- . 1963. Effects of Hurricane Hattie on the British Honduras reefs and cays, October 30-31, 1961. *Atoll Research Bulletin* 95:1-142.
- . 1969. Ecology and morphology of recent coral reefs. *Biological Reviews* 44:433-498.
- Suchanek, T. H. 1979. The *Mytilus californianus* community: Studies on the composition, structure, organization, and dynamics of a mussel bed. Dissertation. University of Washington, Seattle, Washington, USA.
- Sutherland, J. 1970. Dynamics of high and low populations of the limpet *Acmaea scabra* (Gould). *Ecological Monographs* 40:169-188.
- Thompson, D'A. W. 1917. *On growth and form*. Cambridge University Press, Cambridge, England.
- Thompson, R. J., and B. L. Bayne. 1974. Some relationships between growth, metabolism and food in the mussel *Mytilus edulis*. *Marine Biology* (Berlin) 27:317-326.
- Thomson, W. T. 1981. *Theory of vibration with applications*. Prentice-Hall, New York, New York, USA.
- Timoshenko, S. P., and J. M. Gere. 1972. *Mechanics of materials*. Van Nostrand, New York, New York, USA.
- Tunncliffe, V. 1980. Biological and physical processes affecting the survival of a stony coral, *Acropora cervicornis*. Dissertation. Yale University, New Haven, Connecticut, USA.
- . 1981. Breakage and propagation of the stony coral *Acropora cervicornis*. *Proceedings of the National Academy of Sciences (USA)* 78:2427-2431.
- United States Army Corps of Engineers. 1977. *Shore protection manual*. United States Government Printing Office, Washington, D.C., USA.
- United States Navy. 1973. *Summary of synoptic meteorological observations*. National Technical Information Service, Arlington, Virginia, USA.
- Vadas, R. L. 1977. Preferential feeding: an optimization strategy in sea urchins. *Ecological Monographs* 47:337-371.
- Vahl, O. 1973. Pumping and oxygen consumption rates of *Mytilus edulis* L. of different sizes. *Ophelia* 12:45-52.
- Van Valen, L. 1973. Body size and numbers of plants and animals. *Evolution* 27:27-35.
- Vermeij, G. J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecology* 53:693-700.
- . 1978. *Biogeography and adaptation*. Harvard University Press, Cambridge, Massachusetts, USA.
- Vogel, S. 1981. *Life in moving fluids: The physical biology of flow*. Willard Grant Press, Boston, Massachusetts, USA.
- . 1984. Drag and flexibility in sessile organisms. *American Zoologist* 24:37-44.
- Vogel, S., and M. LaBarbera. 1978. Simple flow tanks for research and teaching. *BioScience* 28:638-43.
- Vosburgh, F. 1977. The response to drag of the reef coral *Acropora reticulata*. Pages 477-482 in *Proceedings of the Third International Coral Reef Symposium*. Volume 1, Biology. Rosentiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA.
- . 1982. *Acropora reticulata*: Structure, mechanics and ecology of a reef coral. *Proceedings of the Royal Society of London B Biological Sciences* 214:481-499.
- Wainwright, S. A., W. D. Biggs, J. M. Currey, and J. D. Gosline. 1976. *Mechanical design in organisms*. John Wiley and Sons, New York, New York, USA.
- Wainwright, S. A., and Koehl, M. A. R. 1976. The nature of flow and the reaction of benthic cnidaria to it. Pages 5-21 in G. O. Mackie, editor. *Coelenterate ecology and behavior*. Plenum, New York, New York, USA.
- Went, F. W. 1968. The size of man. *American Scientist* 56:400-413.
- Wiegel, R. L. 1964. *Oceanographical engineering*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- . 1972. Ocean wave spectra, eddies, and structural response. Pages 531-586 in E. Naudascher, editor. *Flow-induced structural vibrations*. Springer-Verlag, Berlin, Germany.
- Wilson, D. S. 1975. The adequacy of body size as a niche difference. *American Naturalist* 109:769-784.
- Woodley, J. D., E. A. Chornesky, P. A. Clifford, J. B. C. Jackson, L. S. Kaufman, N. Knowlton, J. C. Lang, M. P. Pearson, J. W. Porter, M. C. Rooney, K. W. Rylaarsdam, V. J. Tunnicliffe, C. M. Wahle, J. L. Wulff, A. S. G. Curtis, M. D. Dallmeyer, B. P. Jupp, M. A. R. Koehl, J. Neigel, E. M. Sides. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749-755.
- Yule, A. B., and G. Walker. 1984. The adhesion of the barnacle, *Balanus balanoides*, to slate surfaces. *Journal of the Marine Biological Association of the United Kingdom*. 64:147-156.
- Zar, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Zaret, T. M., and W. C. Kerfoot. 1975. Fish predation on *Bosmina longirostris*: Body size selection versus visibility selection. *Ecology* 56:232-237.

APPENDIX 1

Symbol	Definition	Units	Eq. where first used	Symbol	Definition	Units	Eq. where first used
A_b	Basal area of model or organism	m ²	20	$P_{(H>H')}$	Probability that a wave has a height > H'	...	46
A_c	Critical area	m ²	2	P_s	Probability of survival	...	30
A_p	Projected area (direction of flow)	m ²	1	$P_{s,cum}$	Cumulative probability of survival	...	31
$A_{p,max}$	Maximum projected area	m ²	42	P_U	Probability of encountering velocity U	...	44
$A_{p,min}$	Minimum projected area	m ²	42	P_{U_i}	Probability of encountering velocity in range U_i	...	48
B	Proportionality constant	...	3	$P_{(U>U')}$	Probability that a wave has a velocity > U'	...	47
C_a	Added mass coefficient	...	12	r_i	Radial distance to port i	m	11
C_d	Drag coefficient	...	7	Re	Reynolds number	...	9
C_l	Lift coefficient	...	8	s	Standard deviation of breaking stress	N/m ²	30
C_m	Inertia coefficient	...	6	t	Time	s	14
C_p	Center of pressure	m	11	T	Relative thickness (of coral blade)	...	28
D	Specimen length (coral)	m	13	T	Period of oscillation	s	10
d	Distance from neutral axis	m	23	U	Water velocity	m/s	1
F	Loading force	N	13	U_m	Maximum water velocity in oscillatory flow	m/s	10
F_a	Acceleration reaction	N	4	V	Volume of displaced fluid	m ³	4
F_d	Drag force	N	1	y	Distance from neutral axis	m	13
F_{df}	Total force in direction of flow	N	4	W	Relative width (of coral blade)	m	28
F_l	Lift force	N	8	x	Distance from leading edge	m	15
g	Acceleration due to gravity	m/s ²	14	Z	Water depth	m	14
H	Wave height	m	14	α	Angle relative to mainstream velocity	degrees	11
H_{rms}	Root mean square wave height	m	46	δ	Boundary layer height	m	15
ΔH_i	Pressure head at port i	m	11	ν	Kinematic viscosity of water	m ² /s	9
I	Second moment of area	m ⁴	13	ρ	Density of water	kg/m ³	6
K_i	Proportionality constant	...	22	σ, σ'	Stress (force/area)	N/m ²	2, 30
K	Period parameter	...	10	$\bar{\sigma}$	Average breaking stress	N/m ²	30
L	Characteristic length	m	5	$\sigma_{eq,max}$	Equivalent maximum stress	N/m ²	42
L_h	Height of coral blade	m	28	σ_n	Normal stress	N/m ²	23
L_r	Radius of animal or replica	m	18	$\sigma_{n,max}$	Maximum normal stress	N/m ²	24
$L_{r,max}$	Maximum radius	m	26	$\sigma_{s,max}$	Maximum shear stress	N/m ²	21
m	Mass	kg	12	ϕ	Cone angle	degrees	11
M	Moment (force × distance)	Nm	23				
N	Number of pressure ports, waves encountered	...	11, 44				
P_a	P_d due to acceleration	...	32				
P_A	Probability of encountering acceleration A	...	44				
P_b	Size-independent P_d	...	32				
P_d	Probability of dislodgement	...	30				
$P_{d,cum}$	Cumulative P_d	...	31				

APPENDIX 2

Any change in the constants or coefficients appearing in Eqs. 26 and 27 causes the estimate of maximum size to vary. The relative sensitivity of $L_{r,max}$ to variations in $C_d, C_m, C_b, U, \sigma_{max}$, and dU/dt may be assessed as follows. $L_{r,max}$ as defined by Eq. 26 is

$$L_{r,max} = (\sigma_{s,max} - K_1 \rho U^2) / (\rho K_2 dU/dt),$$

and, for $K_1 = (1/3)C_d$ and $K_2 = (8/9)C_m$ (values for a hemisphere),

$$L_{r,max} = (\sigma_{s,max} - [\rho/3]C_d U^2) / ([8\rho/9]C_m dU/dt).$$

The total change in $L_{r,max}$ is

$$\begin{aligned} dL_{r,max} = & (\partial L_{r,max} / \partial \sigma_{s,max}) d\sigma_{s,max} \\ & + (\partial L_{r,max} / \partial C_d) dC_d \\ & + (\partial L_{r,max} / \partial C_m) dC_m \\ & + (\partial L_{r,max} / \partial U) dU \\ & + (\partial L_{r,max} / \partial dU/dt) d^2U/dt^2. \end{aligned}$$

For small errors such that

$$dL_{r,max} \cong \Delta L_{r,max} \ll L_{r,max} \quad (\text{at any } \sigma_{s,max}, C_d, C_m, U, \text{ and } dU/dt),$$

$$d\sigma_{s,max} \cong \Delta \sigma_{s,max} \ll \sigma_{s,max} \quad (\text{at any } L_{r,max}, C_d, C_m, U, dU/dt),$$

etc., for C_d, C_m, U , and dU/dt ,

we may linearize the above equation as:

$$\begin{aligned} \Delta L_{r,max} = & (\partial L_{r,max} / \partial \sigma_{s,max}) \Delta \sigma_{s,max} \\ & + (\partial L_{r,max} / \partial C_d) \Delta C_d \\ & + (\partial L_{r,max} / \partial C_m) \Delta C_m \\ & + (\partial L_{r,max} / \partial U) \Delta U \\ & + (\partial L_{r,max} / \partial dU/dt) \Delta dU/dt. \end{aligned}$$

This defines the absolute variation in $L_{r,max}$; of more interest is the relative variation $\Delta L_{r,max} / L_{r,max}$:

$$\begin{aligned} \Delta L_{r,max} / L_{r,max} = & (\partial L_{r,max} / \partial \sigma_{s,max}) (\Delta \sigma_{s,max} / L_{r,max}) \\ & + (\partial L_{r,max} / \partial C_d) (\Delta C_d / L_{r,max}) \\ & + (\partial L_{r,max} / \partial C_m) (\Delta C_m / L_{r,max}) \\ & + (\partial L_{r,max} / \partial U) (\Delta U / L_{r,max}) \\ & + (\partial L_{r,max} / \partial dU/dt) (\Delta dU/dt / L_{r,max}). \end{aligned}$$

When these partial derivatives are taken and $A \equiv 3(\sigma_{s,max} - [\rho/3]C_dU^2)$,

$$\begin{aligned} \Delta L_{r,max}/L_{r,max} = & \sigma_{s,max}/A \\ & + (U^2\rho\Delta C_d)/3A + (\rho C_d U \Delta U)/3A \\ & + (\Delta dU/dt)/(dU/dt) + \Delta C_m/C_m. \end{aligned}$$

Thus, a 10% variation in dU/dt or C_m will always produce a 10% variation in $L_{r,max}$. In contrast, the relative variation in $L_{r,max}$ caused by a 10% variation in $\sigma_{s,max}$, C_d , or U depends on the magnitude of $\sigma_{s,max}$, C_d , and U . For example a 10% variation in C_d causes a 0.14% variation in $L_{r,max}$ for a well streamlined organism with a very strong adhesive under severe flow conditions ($U = 20$ m/s, $C_d = 0.1$, $\sigma_{s,max} = 10^6$ N/m²). In contrast, a 10% variation in C_d will cause a 58% change in $L_{r,max}$ for a bluff organism with a very weak adhesive under mild flow conditions ($U = 5$ m/s, $C_d = 1.0$, $\sigma_{s,max} = 10^4$

N/m²). A typical example from this study would be the limpet *C. digitalis* moving in moderate to high flow ($U = 10$ m/s, $C_d = 0.52$, $\sigma_{s,max} = 1.29 \times 10^5$ N/m²), for which a 10% variation in C_d would result in a 1.6% variation in $L_{r,max}$.

A similar sensitivity analysis can be carried out for Eq. 27 and is presented here without derivation.

$$\begin{aligned} B & \equiv (32/9\pi)\rho C_m dU/dt, \\ \Delta L_{r,max}/L_{r,max} & = (\Delta\sigma_n/B) + (0.028 U^2\rho\Delta C_l/B) \\ & + [(4/3\pi)\rho U^2\Delta C_d/B] \\ & + \{2U\rho[0.028C_l + (4/3\pi)C_d]\Delta U/B\} \\ & + [\sigma_n - U^2\rho(1/2 - 0.472 + 4/3\pi) \\ & \quad \cdot \Delta C_m/(BC_m^2)] \\ & + \{[\sigma_n - U^2\rho(1/2 - 0.472 + 4/3\pi)] \\ & \quad \cdot (\Delta dU/dt)/[B(dU/dt)^2]\} \end{aligned}$$