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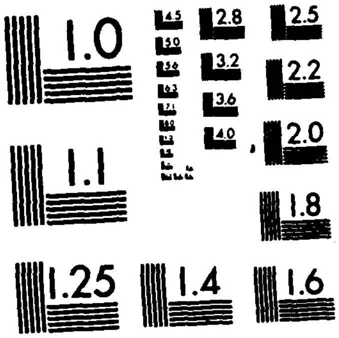

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It is proposed that wave forces, specifically the inertial force due to water acceleration, limits the sizes of wave-swept organisms. A model is provided which predicts the probability of dislodgement based on empirically measurable parameters. This model is tested using various wave-swept species, and in several cases is believed to be applicable. A method is outlined for predicting survivorship as a function of size, and applications of this method are examined.

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MECHANICAL LIMITS TO SIZE IN WAVE-SWEPT ORGANISMS

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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 mechanical limitations have never been thoroughly explored. It is thus possible that the observed limits to size in wave-swept organisms are due solely or in part to mechanical, rather than biological, factors. This possibility is examined.

The total force imposed on an organism in flowing water is due both to the water's velocity and to 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 (the acceleration reaction) increases faster than the organism's structural strength as the organism grows, and thus forms a potential mechanical limit to its size. This fact is incorporated into a model that predicts the probability that an organism will be destroyed (by breakage or dislodgement) as a function of five parameters that may be empirically measured:

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 is tested using a variety of organisms. For each, parameters 1-4 are measured or calculated; the probability of destruction, and the size-

specific increment in this probability, are then predicted. In the cases of the limpets, Collisella pelta and Notoacmaea scutum, the urchin, Strongylocentrotus purpuratus, the mussel, Mytilus californianus (when solitary), and the hydrocoral, Millepora complanata, the probability of destruction and the size-specific increase in the risk of destruction are both 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, Thais 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.

Aside from providing evidence regarding the mechanical limits to size of wave-swept organisms, the model constructed here provides an experimental 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, the length of the 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 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 can attain large sizes (2-3 m in maximum dimension). The precise role of these factors awaits further research.

Key Words. mechanical limits, size limits, wave forces, intertidal organisms, corals, acceleration reaction, added mass, size-specific mortality, exposure, disturbance.

10 Year Index Entries. Mechanical limits to size of wave-swept organisms, quantitative measurement of exposure, size-specific incremental risk of dislodgement, size-specific mortality, size-specific force due to water acceleration, probability of dislodgment, contributions of biomechanics to ecology.

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). Various patterns have been noted in the ecological roles of organisms of different sizes (Hutchinson and MacArthur 1960, VanValen 1973, Kerr 1974, Banse and Mosher 1980, Silvert and Platt 1981, but see Frost 1980) and in the size distribution of organisms through evolutionary time (e.g., Bonner 1968, Gould 1966, Stanley 1973). Basic "rules" for the dependence on body size of the rates at which organisms function (e.g. respire, capture food, grow, or reproduce) have been noted, and various explanations have been suggested (see Schmidt-Nielsen 1974, McMahon 1975a, 1980, Banse and Mosher 1980, Gray 1981, Platt and Silvert 1981, and references cited therein). Organisms of grossly different size often live in different physical realms (e.g., Haldane 1928, Went 1968, Horn et al. 1982). From the many important questions related to the size of organisms we have chosen to examine the mechanical factors which may define the upper boundary to size.

Upper Limits to Body Size

Factors imposing physical upper limits to size have received considerable attention. Since the volume of an organism is proportional to $[\text{length}]^3$, whereas the surface area for exchange of materials as well as the cross-sectional area of skeletal elements (and hence their strength) are both proportional to $[\text{length}]^2$, the shapes of many large organisms are different from small ones in ways that permit area to keep pace with volume (e.g., Haldane 1928, Thompson 1917, Gould 1966, Stanley 1973, Schmidt-Nielsen 1974). Such allometric changes in morphology with increase in body size eventually lead to structural absurdities (Gould 1966): at large body sizes skeletons would deflect too much, break, buckle, or be too bulky to be moved (e.g., Galilei 1638, Haldane 1928, Gould 1966, Currey 1970, MacMahon 1973). The mechanical practicality or the metabolic cost of various types of locomotion (running, swimming, flying, burrowing) may set physical limits to the sizes of various organisms (e.g., Gould 1966, Bonner 1968, Maynard-Smith 1968, Alexander 1971, Stanley 1973, Schmidt-Nielsen 1974, for examples see Pedley 1977). And, as we discuss later, many other factors have also been proposed to limit the size of organisms.

Here we examine size limits of organisms that live in wave-swept environments, in particular those organisms that inhabit the intertidal zone of rocky shores and coral reefs. Wave-swept shores are undoubtedly a physically harsh environment, and, as such, should form an ideal testing ground for an examination of the role played by the physical environment in limiting size, and thereby, for the role played by this one aspect of the environment in the ecology of these organisms.

Wave-Swept Organisms Are Not Large

One simple observation forms the basis for this examination: 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 to 3 m in their greatest dimension) much smaller than the largest organisms on the face of the earth (whales; Sequoia trees (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 are larger in those intertidal areas where wave action is lower (Harger 1970,1972), or subtidally (Paine 1976a,1976b) where the intensity of water motion is less. The same trend has been noted for starfish (Paine 1976a). Many algae are stunted in high wave exposure (Schwenke 1971, Connell 1972), although there are exceptions to 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 sections of reefs (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? There are many biological factors which 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. These limits have never been defined for wave-swept organisms, and it is thus quite possible that apparent biological limits are artefacts. Consequently, in this study we postpone until the Discussion the consideration of biological interactions, and examine instead the hypothesis that there are <u>purely</u> <u>mechanical</u> limits to the size to which organisms may grow in wave-swept environments. There is considerable evidence which supports this hypothesis, showing that large organisms are indeed more likely to be ripped off hard substrata by waves than are small ones (*e.g.* 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, and other rocky shore organisms, see Connell 1972). Once this hypothesis has been evaluated, the role played by biological interactions can be examined more objectively.

The Role of Acceleration

The basis of our argument is a consequence of the unsteady, accelerational nature of the 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 (e.g. Jones and Demetropoulos 1968, Branch and Marsh 1978, for exceptions see Carstens 1968, Koehl 1977a). This force is the drag force, F_d:

$$F_d \propto A_p U^2 \tag{1}$$

where A_p is the area of the organism exposed to flow, projected in the direction of flow, and U is water velocity. 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/area, σ) placed on the organism's structural material is:

$$\sigma = F_d/A_c \propto (A_p/A_c)\, U^2 \tag{2}$$

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

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

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, but the area over which this force is applied is proportionally larger as well, 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 such that 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

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

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, Daniel 1982). If we divide this equation by the critical area over which the force is applied and assume that the organism's volume = $\underline{L}\ \underline{A_c}$ where $\underline{L}$ is thus defined as a characteristic length, the stress on the organism is:

$$\sigma = F_{df}/\underline{A_c} = \underline{B}\ \underline{U}^2 + \underline{B'}\ \underline{L}\ d\underline{U}/d\underline{t} \qquad (5)$$

where $\underline{B}$ and $\underline{B'}$ 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 acclerational flow if $\underline{L}$ exceeds a certain value, exceeds the stress that the organism can sustain (the breaking stress) and the ganism dislodges or breaks. In this manner accelerating flow acts to set a po tial mechanical limit to size.

In order to examine this possibility we:

1. Create a model for the stresses placed on wave-swept organisms,

2. Estimate the flow regime present on wave-swept shores,

3. Measure the necessary hydrodynamic coefficients and constants for actual wave-swept organisms,

4. Measure the distribution of adhesive tenacity for various wave-swept species, and

5. Apply the principles of the model to these species.

MATERIALS, METHODS, AND INTERMEDIATE RESULTS

The exposed rocky shoreline of Washington State and a coral reef in the western Caribbean were chosen as model systems in which to test this theory of size limitation. The majority of the empirical measurements made were carried out at various sites on Tatoosh Island, Washington (124°44'W, 48°23'N). The principal site is a rock face inclined approximately 35° from horizontal and fully exposed to to the prevailing southwesterly swells. The bottom slopes steeply down from the site reaching a depth of 10m (below MLLW) approximately 30m offshore. This depth is maintained for another 70m out from the site before the bottom again slopes steeply downward. Depths of 80-100m are reached within 500m of the site. Other measurements were conducted in various surge channels on Tatoosh. Further intertidal measurements were made at Mukkaw Bay (approximately three kilometers south of Tatoosh Island), and at Shi-Shi Beach (approximately 8 kilometers 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 (78°43'W,9°34'N). As with any intertidal site, the fine-scale topography of the sites used in this study is so complex that a detailed description is 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 models of a limpet (*Collisella pelta*) and on spheres (1 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 where the most violent waves occurred (November 19-20, 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 was used to calculate time vs. velocity and time vs. acceleration records by numerically solving a rearrangement of eq 4:

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

using a fourth order Runge-Kutta method with the boundary condition that all force at zero time is due to the acceleration reaction. 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 discussed below. The density of seawater, ρ, is assumed to be constant at 1025 kg/m^3.

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 the course of this study low tides suitable for installing the telemetry system did not coincide with any severe storms, and the records obtained are thus of waves of less than maximum size. On the other hand, 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, are approximately 14 m/s and 400 m/s^2. This 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 about 4 ms. The response time of the transducer used is 8 ms (Denny 1982), so it is very likely that the transducer's deflection lagged behind the force applied and that the forces measured here are underestimates. Consequently the velocities and accelerations calculated will be underestimates of the actual values for the relatively mild conditions encountered and thus may considerably underestimate the conditions accompanying storm waves. Rather than guessing at one specific maximum velocity and acceleration we use the values calculated here as a rough guide to the lower limit of what the actual maxima are, and present data for velocities from 0 to 20 m/s and accelerations from 0 to 2000 m/s^2. At present we have no independent evidence to confirm this range of accelerations, however there is confirming evidence for the range of velocities. Naval records of wave heights (U.S. Navy 1973) show that for deepwater waves recorded off southwestern Vancouver Island (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 will be shown below (eq. 14), the estimated maximum water velocity at the moment the wave breaks for a 9.75 m wave is approximately 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 three species of locally abundant and characteristic shelled animals (an acorn barnacle, *Semibalanus cariosus*, a limpet, *Collisella pelta*, and a snail, *Thais (Nucella) canaliculata*). 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, $\underline{F_{df}}$, or the force perpendicular to water movement, *i.e.* lift, $\underline{F_l}$. 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 such that the object was held within 1 - 2 mm of the wall. Each object was then subjected to steady water velocities up to approximately 4 m/s. Assuming the flow to be fully turbulent, the boundary layer in the vicinity of the model is calculated to be < 5 mm (see equation 15). Mainstream velocities in the test section of the flow tank were measured with an electromagnetic flowmeter (Cushing Velmeter 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. The resulting area was cut out, weighed, and compared to the weight of standard areas to arrive at the final estimate of projected 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):

$$C_d = 2F_d/(\rho A_p U^2) \tag{7}$$

$$C_l = 2F_l/(\rho A_p U^2) \tag{8}$$

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 value which is a measure of the relative contribution of inertial and viscous processes in determining flow patterns around objects:

$$Re = U L/\nu \tag{9}$$

where U is the velocity of the fluid relative to the organism, L is a characteristic length which we take to be the diameter of the organism, and ν is the fluid's kinematic viscosity ($1 \times .10^{-6}$ m ^{2}/s) (Figure 1). The values used here are those obtained for Reynolds numbers around 10^5 (equivalent to a velocity of 10 m/s for an object 1 cm long), a value generally approriate for the conditions encountered during breaking waves. A variety of water velocities and sizes of objects are used in this study, corresponding to Re`s both higher and lower than the standard Re used to estimate C_d and C_l. Thus the values may slightly over- or underestimate the actual C_d and C_l values in any given situation. This 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 measured here. As Vogel (1981) observes, the variation of C_d with Re decreases as the irregularity of the object increases; thus for an organism such as a sea urchin, C_d may vary little with Re. The C_d of plate-like organisms (such as the coral species discussed later) varies only insignificantly (<5%) over the Re range of $10^3 - 10^6$ (Hoerner 1965). The effect of variations of C_d and C_l is examined more closely in the Discussion and in Appendix 2. The C_d and C_l values used here were measured in steady flow. If, instead, 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 either using the values presented by Hoerner(1965) or by assuming values equal to those of an object of similar shape. For example, values for the acorn barnacle *Balanus glandula* are assumed to be equal to those of *S. cariosus* for which measurments 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 = 0.5, 1.0, 2.0 respectively) were turned from acrylic plastic. In each, five ports (approximately 1 mm diameter) were drilled in a line running from the basal edge up to and including the apex (see Figure 2). Each cone was attached to the top wall of the flow tank and exposed to a steady velocity of 0.63 m/s ($\underline{Re} = 6.9 \times 10^4$). 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 ($\rho_m = 1594$ kg/m^3) as the manometer fluid. Readings were taken with the row of ports at angles to the water flow varying 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, $\underline{C_p}$:

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

The definition of terms is shown in Figure 2.

The center of pressure was found to lie along the midline and downstream of the apex by distances varying between 0.111 $\underline{L_r}$ (for the cone with height/radius = 2) and 0.29 $\underline{L_r}$ (for the cone with height/radius = 0.5), where $\underline{L_r}$ is the cone radius. The average location of the center of pressure was 0.24 $\underline{L_r}$ downstream of the apex, and this value is used in the calculations here.

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 is accounted for by use of an added mass coeficient, α . 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, Inc.) to provide rigid, light models. The models were coated with spray paint to prevent waterlogging and the mass of each model was measured on an electric balance to ± 0.001 g. The mass of water each model displaced when immersed was determined by measuring the bouyant force exerted by submerged models. The mass of displaced fluid was measured to ± 0.05 g.

Models were 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 model was accomplished by suspending the force platform from the ceiling with wires approximately 5 m long and allowing the platform to swing like a pendulum. The model and rod were at all times immersed in a long trough of water. Acceleration of the model was measured using an accelerometer (Entran Devices type EGA-125) mounted on the tip of the rod next to the model. 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 models. Since these intertidal animals are normally attached to the substratum we chose to accelerate our models parallel to a boundary 1 - 2 mm from the base of each model.

Since the velocity of the model was small during the initial stages of acceleration (less than 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 models can be expressed in a form similar to eq. 4.

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

where F_{df} is the total force, α is the added mass coefficient, V is the volume of fluid displaced by the model, m is the mass of the model 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 the above equation.

For all equations that follow an inertia coefficient is defined for stationary oganisms in accelerating flows as $Cm = 1 + \alpha$ to include the effects of virtual buoyancy (Batchelor 1967, pg. 409), and values are shown in Table 1.

Tenacity and Breaking Strength Measurements

The adhesive tenacity, σ_{max}, expressed as the force per area required to dislodge the organism, was measured for eight species of intertidal animals. Tenacity measurements for six of these species (Collisella digitalis, B. glandula, S. cariosus, Balanus nubilus, Mytilus californianus, and Strongylocentrotus purpuratus) were made on the exposed coast of Washington at Tatoosh Island or Shi-Shi Beach, and the other species (C. pelta, and Notoacmaea scutum) were measured at the Friday Harbor Marine Laboratory in Puget Sound. All animals tested were solitary, i.e. they were fully exposed to the prevailing flow and were not shielded by their neighbors. The outer coast measurments 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. 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, was estimated as the length-width product. 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 of 1.42 is 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, the stress at which the material would break, is 1.33 or 1.50 times the average stress (force/basal area) depending on whether the base is circular or rectangular (Timoshenko and Gere 1972). Since the animals measured here are generally intermediate between these two shapes an average value of 1.42 was chosen. The shapes of the organisms measured in this manner make this method possible by preventing the string loop from slipping off when force is applied (eg. the overhanging apex of the shell of C. digitalis). The two remaining limpet species were less accommodating, requiring a different technique. Measurements made on C. pelta and N. scutum at Friday Harbor were made using a strain gauge force transducer similar to that described by Denny (1982). A short piece of wire bent into a hook was glued to the shell apex using quick-setting epoxy glue. The force transducer was then attached to the hook and force 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 all were tapped or otherwise bothered slightly immediately before testing to induce the animal to adhere as best it could.

The values of tenacity measured in this study, as well as values from 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 moving tenacity of limpets are somewhat suspect since the values reported for stationary limpet tenacity measured under similar conditions in the laboratory (i.e. for animals adhering to acrylic plastic) are substantially lower than the values of other authors determined in the field. Assuming that the ratio of moving to stationary tenacitites as measured by Miller (1974) are accurate, we have estimated the tenacity of moving limpets by multiplying the field-determined stationary tenacity values for each species by the average ratio of moving to stationary tenacity for all species using ditaxic waves, 0.334 (as determined by Miller 1974).

The breaking strength of the hydrocoral Millepora complanta 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 Panamá. The corals were cut into strips approximately 1 cm wide using a diamond saw; strips were cut parallel to the long axis of each coral blade. For each test the sample was simply supported near its ends, the distance, D, between supports measured, and a bucket suspended by a wire from the centerline of the sample. Water was added to the bucket and the force acting on the sample thus 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),

$$\text{modulus of rupture} = D\,F\,y/\,4I \qquad (13)$$

where F is the mass of the bucket and water multiplied by the acceleration of gravity (9.81 m/s^2), y is 1/2 the thickness of the sample, and I is the second moment of area of the cross-section (= [2/3] width y^3) for a rectangular cross-section. The modulus of rupture for the 39 samples tested was 1.23×10^7 N/m^2 ± 1.47×10^6 N/m^2 (95% confidence intervals).

Dimensions of Mussels

Mussels were collected for morphological measurements from a 0.25 m square 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 their volume was measured to the nearest 0.1 ml by immersing each mussel in a graduated cylinder containing water.

Fifty mussels of various sizes were pulled off the exposed rock surface at Tatoosh Island, the force of dislodgement being measured as described above. A plot of dislodgement force vs. length of the mussel (Figure 3) shows that the adhesive tenacity increases in proportion to $L^{1.95}$. A length vs. volume plot for 182 mussels from Tatoosh (Figure 4) shows that volume increases as $L^{2.86}$. Assuming that projected area is proportional to the 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, as assumed for the model discussed later.

If a mussel is treated as a streamlined body with a thickness of approximately half its length, its $\underline{C_d}$ is about 0.2 when end on to the flow and 0.8 when broadside at the $\underline{Re}$ expected during wave flows (Hoerner, 1965), and these values are used here. $\underline{C_m}$ is approximately 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, $\underline{A_{p,min}}$, is used to calculate an "equivalent stress" (force of dislodgement/$\underline{A_{p,min}}$) (Table 1).

WATER FLOW IN WAVE-SWEPT HABITATS

Before discussing the theory 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.

Intertidal organisms are exposed to breaking waves and post-breaking 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 (e.g. Cokelet 1977, 1979, Peregrine 1983, Longuet-Higgins 1982, Stive 1980). It is possible however to draw a general, approximate, picture of these flows. A wave approaching shore breaks when the height of the wave above still water level 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. With gradually sloping bottoms waves curl over and the crest plunges forward at breaking; these conditions apply for 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 of the type termed "spilling" 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 travels with a velocity, $\underline{U}$, parallel to the bottom, given as a first approximation by linear wave theory as:

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

where $\underline{g}$ is the acceleration due to gravity (9.8 m/s^2) and $\underline{H}$ and $\underline{Z}$ are the wave height and water depth respectively (Weigel 1964). Thus, for a five meter wave breaking in water five meters deep the crest velocity is approximately 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 emersed rocks of the shore. In such a case, water with velocity into 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 experience (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 (3) an impulsive onrush of a wave front 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 non-breaking waves and should not be used as an estimate of fluid accelerations once a wave has broken and run shoreward. Carstens (1968) also explores the pressures associated with the impingement of a jet on an impermeable surface. These impact pressures may be quite large, with values exceeding 1.5×10^7 Pa. Organisms exposed to such pressures may fail by implosive rupture rather than being sheared off the rock wall. The magnitude of impact pressures 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 its value with no entrained air (Carstens, 1968). Since Longuet-Higgins and Turner (1974) estimate an air content of about 10% for spilling breaking waves, impact pressures may be nearly an order of magnitude lower than that 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 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. 5). Because the flow is not directed into the substratum there will be no substantial 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 make one crucial assumption: the fluid speed and acceleration at any instant in time do not change as a function of distance from the substratum. Thus, we assume the kinematics of the flow encountered by an organism to be independent of body size. Clearly, there are situations in which this assumption is violated as will be discussed in a later section of this paper. However, we believe this assumption to be a valid first approximation for solitary organisms. This conclusion is based on the following reasoning:

1) The establishment of a boundary layer requires time. Is there sufficient time during the onrush of breaking wave for viscosity to result in the build-up of a significantly large boundary layer? This question is not relevant to "steady" turbulent flows, and the problem, here, is to estimate the growth in time of a turbulent boundary layer. 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 which relates boundary layer thickness to the distance of a point from the leading edge of a flat plate:

$$\delta = 0.37\ x\ (\underline{U}\ \underline{x}/\underline{\nu})^{0.2} \tag{15}$$

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

$$\delta = 0.37\ \underline{U}^{0.6}\ \underline{t}^{0.8}\quad {}^{0.2} \tag{16}$$

Using Figure 5 to provide numerical estimates of the values in the above equation and assuming a kinematic viscosity of 10^{-6} m^2/s we calculate that the boundary layer would build up to its maximum thickness of only 5 x 10^{-3} m ($t \simeq 0.05$ s, $U \simeq 5$ 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 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 velocity gradient is steepest in a region confined to a small distance from the boundary. 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 greater than 50% of the free stream velocity. From 20% of the boundary layer thickness outwards, the velocity changes only by a factor of about 25%. (See Fig. 18.5 in Sclichting 1979). Consequently, our assumption of a constant velocity is reasonable for turbulent boundary layers even as thick as 1 or 2 cm. Thus, owing to the very short duration of the initial surge, and to the nature of turbulent boundary layer profiles our assumption appears valid that the flow encountered by macroscopic solitary organisms is independent of body size.

The force trace from one large breaking wave is shown in Figure 5, 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 thirty waves for which calculations were made, no significant correlation exists between maximum acceleration and the velocity at which that acceleration occurred ($r = 0.022$, $N = 30$, $P > 0.5$.)

MODELS

Here we examine the hydrodynamic forces that act on a simple general model of a wave-swept organism as shown in Figure 6. The model "organism" is a hemisphere of radius L_r attached to a planar surface. The passage of a wave causes water to flow along the surface and past the organism, placing a number of forces on the body. In the direction of flow (*i.e.* parallel to the surface plane) there is a force, F_{df} which 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 . By rearranging eq. 7 it can be seen that F_d varies with velocity, U:

$$F_d = 0.5 \rho C_d A_p U^2 \tag{17}$$

Thus for the hemispherical model where $A_p = 0.5 \pi (L_r^2)$

$$F_d = 0.25 \rho C_d \pi L_r^2 U^2 \tag{18}$$

The accelerational component is

$$F_a = \rho C_m V \, dU/dt = [2/3] \rho C_m \pi L_r^3 \, dU/dt \tag{19}$$

where V is the volume of the model ($[2/3] \pi L_r^3$). 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 model experiences a force at right angles to the flow and away from the surface, the lift, F_l, which varies with water velocity in a manner similar to drag:

$$F_l = 0.5\rho C_l A_b U^2 = 0.5\rho C_l \pi L_r^2 U^2 \tag{20}$$

where A_b is the basal area of the model (L_r^2). Recall that lift is not centered on area A_b but rather, acts as a point force some distance downstream of center (the center of pressure). Lift in hemispheres attached to walls has not been sufficiently studied to allow precise location of the center of pressure, but assuming that the hemispherical model behaves similarly to the conical models actually 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 the calculations made here.

If the model is to remain stationary and attached to the surface plane, the forces F_a, F_d, and F_l must be resisted by the adhesive which holds the model in place. The forces acting on the adhesive are of two sorts. F_a and F_d tend to push the model 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):

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

Expanding eq. 21:

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

The size of the model, expressed in this case 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 model the greater the shear stress on its basal adhesive.

In addition to a tendency to slide sideways in response to a shear force, the model, as shown in Figure 6, tends 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 model. Unless $M_1 = M_2$ there is some net tendency to rotate the model 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. Depending on its direction, this rotation compresses or extends the adhesive on the upstream half of the base and does the opposite to the downstream half. 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):

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

where $\underline{I}$ is the second moment of area about the neutral axis. For a circular cross-section as in this model $\underline{I} = 0.25\pi \underline{L_r}^4$. The normal stress thus reaches a maximum at the leading and trailing edges of the model where $\underline{d} = \underline{L_r}$. 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 $\underline{F_l}$ is large compared to $\underline{F_{df}}$ (which it is not for the bodies we studied) the effect is minor and has not been included in this analysis. Thus the maximum normal stress, $\underline{\sigma_{n,max}}$, is :

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

Expanding the terms in eq. 2 and rearranging:

$$\begin{aligned}\underline{\sigma_{n,max}} &= 0.5\rho \underline{C_l}\, \underline{U}^2 - .472\, \rho\, \underline{C_l}\, \underline{U}^2 + (4/3\pi)\rho \underline{C_d}\, \underline{U}^2 \\ &\quad + (32/9\pi)\rho \underline{C_m}\, \underline{L_r}\, d\underline{U}/d\underline{t} \\ &= \underline{K_3}\, \rho\, \underline{U}^2 - \underline{K_4}\rho \underline{U}^2 + \underline{K_5}\rho \underline{U}^2 + \underline{K_6}\rho \underline{L_r}\, d\underline{U}/d\underline{t} \\ &= \underline{U}^2\rho(\underline{K_3} - \underline{K_4} + \underline{K_5}) + \underline{K_6}\rho \underline{L_r}\, dU/d\underline{t}\end{aligned} \tag{25}$$

As with the maximum shear stress, the maximum normal stress for a given velocity and acceleration is affected by the size of the model; the larger the radius, the greater $\underline{\sigma_{n,max}}$. By rearranging equations 22 and 25 it can be seen that $\underline{L_{r,max}}$, a measure of the maximum size of the model, is for failure due to shear stress:

$$\underline{L}_{\underline{r,max}} = (\sigma_{\underline{s,max}} - \underline{K}_1 \rho \underline{U}^2)/(\underline{K}_2 \ \rho \ d\underline{U}/d\underline{t}) \tag{26}$$

or for failure due to normal stress:

$$\underline{L}_{\underline{r,max}} = (\sigma_{\underline{n,max}} - \underline{U}^2 \ \rho \ (\underline{K}_3 - \underline{K}_4 + \underline{K}_5))/(\underline{K}_6 \rho \ d\underline{U}/d\underline{t}) \tag{27}$$

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 the model (or an organism similar to the model) 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 may 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 ($\underline{K}_1$ to $\underline{K}_6$) may easily be derived for other shapes such as cones and cylinders, and these values are shown in Table 2.

For certain organisms, some of the forces calculated above are negligible and for these organisms a simplified model 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, $\underline{L}_h$, is much greater than its depth, the length of the moment arm ($\underline{M} = \underline{L}_h/2$) 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 neglect lift forces in the calculation of size:

$$F_{df} = 0.5\,\rho\,C_d\,W\,L_h^2\,U^2 + \rho\,C_m\,W\,T\,L_h^3\,dU/dt \tag{28}$$

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

$$\begin{aligned}\sigma_{n,max} &= My/I \\ &= 3\,(\rho/2T^2)\,C_d\,U^2 + 3\,(\rho/T)\,C_m\,L_h\,dU/dt\end{aligned} \tag{29}$$

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] $WT^3\,L_h{}^4$). Similar calculations may be made for organisms shaped like long, thin cylinders and the appropriate constants are summarized in Table 2.

One final and important addition must be made to these models 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, in any actual species some distribution of breaking strengths is to be expected, and for the organisms examined here, this distribution was found to be indistinguishable from a normal distribution (graphical method, Zar, 1974). 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, σ', of at least a certain magnitude can be specified:

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

where s is the standard deviation, $\bar{\sigma}$ is the mean breaking stress and σ' is the observed 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, the fraction that does *not* have a certain adhesive strength, P_d, (= $1 - P_s$) is a measure of the fraction of the population which *is* dislodged by one particular wave with a given set of flow parameters.

Alternatively, P_s and P_d may be viewed as an estimate 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 argument at hand and is maintained throughout this discussion.

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

$$\begin{aligned} P_{s,cum} &= (P_{s,1} \times P_{s,2} \times \cdots P_{s,N}) \\ P_{d,cum} &= 1 - (P_{s,cum}) \end{aligned} \tag{31}$$

where $P_{s,i}$ is the probability of *not* being dislodged by each individual wave and N is the number of waves encountered. Note that eq. 31 requires that the flow parameters of each of the $\underline{N}$ 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, the application of eq. 31 is difficult. A method for approximating eq. 31 is discussed later.

For an occurrence such as dislodgement or catastrophic breakage it is unlikely that (without actually being dislodged) an organism can "judge" its instantaneous position on its species' breaking strength distribution. Once dislodged, it is too late to act on the knowledge. Thus it would be advantageous, in an evolutionary sense, for an organism to grow only to such a size where, for given flow parameters, its cumulative probability of dislodgement is acceptably small. 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 equation 5 it can be seen that in theory even in steady flow ($d\underline{U}/d\underline{t} = 0$) 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, $\underline{P_b}$. For an organism in accelerating flow there is a stress due to the acceleration reaction that can also be used to calculate a probability, in this case, $\underline{P_a}$, the accelerational component of the probability of dislodgement. Thus

$$\underline{P_d} = \underline{P_b} + \underline{P_a} \tag{32}$$

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 concommittant with an increase in size, dP_d/dL.

$$dP_d/dL = (dP_d/d\sigma') \cdot (d\sigma'/dL). \tag{33}$$

For shear failure (eq. 22)

$$d\sigma'/dL = d(K_2 \rho L_r \, dU/dt + K_1 \rho U^2)/dL = K_2 \rho \, dU/dt \tag{34}$$

or for failure due to normal stress (eq. 25)

$$d\sigma'/dL = d[U^2 \rho (K_3 - K_4 + K_5) + K_6 \rho L_r \, dU/dt]/dL = K_6 \rho \, dU/dt \tag{35}$$

assuming $dC_d/dRe = 0$. From eq. 30

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

$$= s^{-1} (2\pi)^{-1/2} \exp-(\sigma-\bar{\sigma})^2/2s^2) \tag{36}$$

Therefore, for shear

$$dP_d/dL = s^{-1} (2\pi)^{-1/2} \exp-[(\sigma-\bar{\sigma})^2/2s^2] \, (K_2 \rho \, dU/dt) \tag{37}$$

or for failure due to normal stresses

$$dP_d/dL = s^{-1} (2\pi)^{-1/2} \exp-[(\sigma-\bar{\sigma})^2/2s^2] \, (K_6 \rho \, dU/dt) \tag{38}$$

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

$$dP_d/(dL/L) = L \cdot dP_d/dL \tag{39}$$

For failures due to shear stresses

$$L dP_d/dL = s^{-1} \, (2\pi)^{-1/2} \, \exp-[(\sigma-\bar{\sigma})^2/2s^2] \, LK_2 \rho (dU/dt) \tag{40}$$

or for failure due to normal stresses

$$L dP_d/dL = s^{-1} \, (2\pi)^{-1/2} \, \exp-[(\sigma-\bar{\sigma})^2/2s^2] \, LK_6 \rho \, dU/dt \tag{41}$$

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 are 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),

4) and when the stress on the organism is equal to the mean breaking stress. For a given set of flow parameters, $\sigma = \bar{\sigma}$ for one certain 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 for each wave encountered. In such a case it can be reasonably hypothesized that the size of a certain species 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 concommittant with an increase in size. A detailed examination of this interplay is postponed to the Discussion. However, at this point it will be useful to choose a cutoff value for LdP_d/dL above which LdP_d/dL is considered "large". For reasons treated more fully in the Discussion a value of $LdP_d/dL > 0.1$ is considered to be large enough to have limited the size of an organism.

APPLICATIONS OF THE MODEL

We now proceed to examine specific examples of organisms. First we consider four cases in which the basic ideas of the model are born out: sea urchins, limpets, mussels, and one species of hydrocoral.

Sea Urchins

The body of *Strongylocentrotus purpuratus*, the common purple urchin of the Pacific Northwest, consists of a roughly hemispherical rigid test (up to approximately 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 (i.e. Shi Shi Beach) urchins are found fully exposed to the forces of the prevailing waves, and are thus suitable for the analysis described here.

Calculations have been made here for *S. purpuratus* from Shi-Shi beach using the C_d and C_m values shown in Table 1, and the equation for shear stress (Eq. 22).

Figure 7 shows a plot of $\underline{P_d}$ 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 dislodgment is low (< 0.1) but the size-specific increment in $\underline{P_d}$ is large (> 0.3) (Fig. 7b,c). Thus, if these animals experience flows in the range of 1-5 m/s their size may be limited by mechanical constraints.

Limpets

Limpets are small herbivorous gastropods with characteristics conical shells found attached to intertidal rocks on wave-swept shores. During low tides and when disturbed limpets clamp their shell tightly against the rock. At high tide, however, when water flow is greatest, these animals move around to browse algae. The $\underline{C_d}$, $\underline{C_m}$, and $\underline{C_l}$ values used in the calculations made here, along with the values defining the distribution of adhesive tenacities are shown in Table 1. The equation for shear stress (eq. 22) was used for C. digitalis; the equation for normal stress (eq. 25) for C. pelta and N. scutum. Figures 8ai,bi,ci show the $\underline{P_d}$ vs. acceleration curves for the three limpets used in this study at four water velocities. It can readily be seen that stationary limpets, firmly clamped down (dashed lines), run little risk of being dislodged by wave forces. However, when the calculated breaking stress values for moving limpets are used in the calculations (solid lines), both the base probability of dislodgement and the size specific increment in risk are predicted to be much higher. This is most obvious for C. pelta and N. scutum (see Fig 8a and 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 LdP_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 all three species an increase in length above that seen in nature results in an increase in $L\ dP_d/dL$ (Figures 8aii,bii,cii). From these data we conjecture that at high flow rates (> 10 m/s) C. pelta and N. scutum may be mechanically limited to sizes where the stress placed on their adhesives is small enough so that they can tolerate the decrease in adhesive tenacity that accompanies feeding. At flow rates of 1-10 m/s the base probabilities are low (< 0.1) and LdP_d/dL is high (> 0.1) and 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 from the general morphology of urchins and limpets. Rather than having a shell closely applied to the substratum with a large adhesive base, the mussel shell protrudes well above the substratum and is held in place by an array of byssal threads. Despite this difference in morphology it was found that the adhesive strength of M. californianus scales in the same manner relative to body volume and projected area as required for the model described here (eq. 22), and thus the same calculations, with minor rearrangements, may be used. In order to use the equations previously described, the dislodgment force for M. californianus is expressed as an "equivalent stress", σ_{eq}, by dividing force by a calculated projected area, A_p. A_p in turn varies with the direction of flow relative to the mussel's long axis, and is at a minimum ($A_{p,min}$, [in m^2] = 0.126 $L^{1.91}$; L in m) 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 equations appropriate for calculating L_{max} are thus:

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

$A_p/A_{p,min}$ equals 1 when the mussel is end-on to the flow and 2.19 when the mussel is broadside. Using the relationship shown in Figure 4 (V, [in m^3] = 0.061 $L^{2.86}$, L in m)

$$\sigma_{eq,max} \cong 0.5 \rho C_d A_p U^2/A_{p,min} + 0.48 \rho C_m L \; dU/dt \tag{43}$$

Values of P_d are shown in Figure 9 as a function of acceleration. From Figure 19 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. Mussels oriented end-on to the flow present a more feasible picture (Figure 9). Here, 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 may be found oriented in a direction parallel to flow in such habitats on Tatoosh Island. For mussels exposed to flows neither end on nor broadside the force encountered will be intermediate between broadside and end-on values, and P_d and LdP_d/dL likewise will be intermediate. As with the organisms discussed above, the size specific increment in risk for *M. californianus* increases as the size of the animal is increased above that observed in the field (Figure 19).

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 0-4 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 of 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 $L\ d\ P_d/dL$ have been calculated for various velocities and accelerations (Figure 10).

While at velocities high for this reef environment (>10 m/s) the base probability of dislodgement is very high (> 0.8) it is unlikely that waves high enough to cause such velocities (>5m) occur at the site where $L_{h,max}$ was measured. For the maximum wave heights observed at Galeta Point (2-3m, J. Cubit pers. com.) velocities of 7.5 m/s are more likely (eq. 14). At these velocities the base probability is relatively low and $\underline{L}\ d\underline{P}_d/d\underline{L}$ 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, pers. com.) This difference in morphology could be occurring in response to the mechanical limitations cited here.

We now examine six species that are apparent exceptions to the ideas discussed above.

Snails

Data for three species of snails commonly found on Tatoosh Island (Thais canaliculata, Thais emarginata, Littorina scutulata) are shown in Table 1. Probability calculations have been made using the $\underline{C}_d$ and $\underline{C}_m$ values shown in Table 1 and using eq. 22. Compared to the tenacities of limpets, the stationary adhesive strength of these snails is quite low, with the consequence that at rapid water velocities (10-20 m/s) the size-independent probability of dislodgement approaches 1 (see Figure 11). 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 unity for velocities greater than 5 m/s.

For all three species, at moderate flow conditions (5 m/s, < 500 m/s^2) the $\underline{L}\ d\underline{P}_d/d\underline{L}$ values based on stationary tenacity may be substantial. At main stream 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, 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* hidden between acorn barnacles and in crevices in the rock surface. It may be conjectured then that the mechanical environment constrains the behavior of these snails and imposes an indirect limit to 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 limited to times when the environment is mechanically 'safe'.

Acorn Barnacles

The adhesive strength of three species of acorn barnacle (*Semibalanus cariousus, 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 dislodgment is low and the size specific increment in risk even lower (see Figure 12 for S. cariosus). It thus seems unlikely that the size of these organisms is limited by the mechanical factors considered here. However, there might be a mechanical limit to the size of the cirral net, which must be extended into the flow during feeding, and thereby of the whole organism.

DISCUSSION

P_d, LdP_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 survive to reproduce. Equation 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 occurring in the time before an 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 an approximate form of eq. 31 as a tool for comparing the survivorship of organisms of various sizes.

We first examine the case of a motile organism. When an 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 be less strongly adherent, or it may crawl over a clean rock surface and adhere quite well. We assume here that as the organism crawls, its adhesive tenacity always lies within the instantaneous distribution shown by its species at that site, but that the adhesive tenacity of an individual at one time is independent of that at another time. Thus, for times short enough that growth can be neglected the probability of an individual not being dislodged by a wave of given prameters is independent of time and equal to P_s (eq. 31).

Over a period of time N waves strike an individual. Assume that the probability of encountering a velocity within a certain range, U_1, is P_{U_1} for a certain wave, and the probability of encountering an acceleration within a certain range, A_1, is P_{A_1}, for the same wave. Further assume, as suggested by the data cited earlier, that there is not corelation between the velocity and acceleration encountered. Given these assumptions, the number of waves with a velocity and acceleration within these ranges is $NP_{U_1} P_{A_1}$. Equation 31 can thus be approximated as

$$P_{s,cum} = (P_s)^{NP_{U_1} P_{A_1}} \times (P_s)^{NP_{U_2} P_{A_2}} \ldots \times (P_s)^{NP_{U\max} P_{A\max}} \qquad (44)$$

for the total range of velocities and accelerations between U_1 and U_{max} and A_1 and A_{max}. Each P_s is evaluated per 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:

$$P_{s,cum} = \exp\ N \sum_{i=1}^{i_{max}} P_{U_i} \sum_{j=1}^{j_{max}} P_{A_j} \ln P_s \qquad (45)$$

If the probability distributions of P_{U_i} and P_{A_j} 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 (U.S. Army 1977).

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

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. 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 so 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 (Weigel, 1964), eq. 46 can be rewritten as

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

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

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

where U' and U'' are the ends of the range U_i such that $U''>U'$. In making these assumptions we ignore the increase in wave height as deep-water waves shoal.

P_A is unknown. Rather than assuming some probability function, we set the acceleration to a value of 500 m/s^2 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 the Material and Methods these measurements probably underestimate the true values. Equation 45 thus becomes.

$$P_{s,cum} = \exp N \sum_{i=1}^{i_{max}} P_{U_i} \ln P_s \tag{49}$$

where P_s is evaluated for the mean velocity within each range U_i and for an acceleration of 500 m/s^2. Given values for H_{rms}, the hydrodynamic coefficients for the given organism (C_d, C_l, C_m), the population distribution of breaking strengths, and the animal's size an approximation of the probability of surviving the impact of N waves can be calculated.

Equation 49 is based on the assumption that the adhesive tenacity of the individual at one time is independent of that at another time. While this assumption seems valid for moving limpets or snails, it does not seem reasonable for an organism that is permanently cemented in place, such as an acorn barnacle. In this case it seems more reasonable to assume that each organism has an adhesive tenacity that is independent of time. This time-independence can be incorporated into an approximation of Eq. 31 as follows: Consider an organism of fixed, but initially unknown, adhesive tenacity. Before this organism is subjected to wave forces it can only be said that its adhesive tenacity lies within the distribution of adhesive tenacities shown by its species at the particular site being examined. After the organism survives N waves information is available as to the organism's adhesive tenacity: Each of these waves has subjected the organism to a stress, and the organism has not been dislodged. The oganism can thus possess less than a certain value of adhesive tenacity, 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'. Assuming, as before, a value for acceleration, the stress placed on the organism by each wave is determined solely by the 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

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

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

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

For example, given an H_{rms} of 1.0 m the probability that a given wave has a velocity greater than 0.1 m/s is very high (>0.99). Thus, $1 - P_{(U>U')}$ is nearly zero and $[1-P_{(U>U')}]^{N}$ is smaller still. Having encountered N waves and survived there is a very low probability that the organism has 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 is, determined by

$$P_s' = 1-(P_d\,[1-P_{(U>U')}]^{N}) \tag{52}$$

Inserting this adjusted value of P_s' into eq. 49.

$$P'_{s,cum} \cong \exp \sum_{N=0}^{M} \sum_{i=1}^{i_{max}} P_{U_i} \ln P_s' \tag{53}$$

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:

$$P''_{s,cum} \cong \exp \sum_{D=0}^{D_{max}} N \sum_{i=1}^{i_{max}} P_{U_i} \ln \left(1-P_d \left[1-P_{(U>U')}\right]^{ND}\right. \qquad (54)$$

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

As approximations of the exact solution to survivorship (equations 31) equations 49 and 54 can be used to compare survivorship of organisms of different sizes. For present purposes this is done by assuming a constant value for H_{rms} and calculating $P_{s,cum}$ or $P''_{s,cum}$ as a function of time for organism 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 the 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 surf zone 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 have been ignored.

Figures 13 and 14 show the results of applying these approximations to several of the species studied here. Due to their very high base probability of dislodgement, and the likelihood that their size is limited by other than mechanical factors, the snails T. emarginata, T. canaliculta and L. scutulata are not included in this examination.

Animals are assumed to encounter 5000 waves/day. In general a value of $\underline{H_{rms}}$ = 1.0 m has been used, as suggested for exposed shores of the Pacific Northwest by the U.S. Army (1977). For those species occurring in more protected areas (S. purpuratus, M. complanata) the value of $\underline{H_{rms}}$ has been reduced accordingly (0.5 m and 0.25 m respectively). Except where noted eq. 54 (which assumes fixed adhesive tenacity) has been 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 analysis 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. Because such information is not yet available for the animals we are considering here, we present the following simple analysis in order to arrive of a "rule of thumb" for deciding whether mechanical factors are likely to be important in limiting the size of wave-swepth organisms (i.e. for designating $\underline{L}\ d\underline{P_d}/d\underline{L}$ as "large" or "small").

For the sake of simplicity we assume that organisms produce young only once per year, and maintain a constant size throughout the year. For organisms which 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 young or young of a greater viability. In either case it is assumed that for a doubling in linear dimension eight times as many progeny are contributed to the next generation. Given these two 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 the comparative purposes for which it is employed here.

a. A Sea Urchin - *S. purpuratus*: At the end of one year urchins of the maximum size observed at Shi Shi Beach are 41 times more likely to have survived than urchins of twice this size (Figure 13a). Conversely, 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 on the criterion cited above, it appears feasible that due to mechanical factors a selection pressure exists limiting the size of this urchin.

b. A Mussel - *Mytilus californianus*: At the end of one year a mussel oriented broadside to the flow is 156 times more likely to survive at the maximum size observed on Tatoosh island than at twice that size (Figure 13b). A mussel half the observed maximum size is only 4.4 times as likely to survive as at the maximum observed size. Thus mussels oriented broadside to its flow could be limited by mechanical factors. However, for mussels oriented end-on to the flow the observed maximum size is only 5.6 times as likely to survive as a mussel twice this size (Figure 13e). Due to the unpredictable direction of flow in natural environments, any given mussel is oriented neither precisely end-on nor broadside to most waves. The appropriate survivorship ratio thus lies somewhere between 156 and 5.6 and is likely to be greater than 8. It seems feasible that the size of solitary M. californianus is limited by mechanical factors.

c. A Coral - Millepora complanata: After only one month's exposure to waves with $\underline{H_{rms}}$ of 0.25 m a coral blade of the maximum size observed on the Galeta reef is 90 times more likely to remain intact than a blade twice the observed size (Figure 13c). At the end of a year this ratio is 1700. In contrast to mussels and urchins, however, a coral blade that is half the observed maximum size is approximately 16 times as likely to survive as is a blade of the maximum observed size and one might be led to conclude that a selection pressure exists for this coral to be smaller than actually observed.

Two factors must be taken into account when examining these results: 1) The reproductive output of M. complanata (when reproducing sexually) is probably more a function of the volume of polyps rather 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, i.e. 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. complanta occasionally land on favorable substratum, re-attach and grow (pers. obs.). Breakage may thus serve as a dispersal mechanism (Highsmith 1982). These two factors lead to different possible interpretations of the results. 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 place a stronger selection pressure against increased size *if* breakage results in death. However, if an increased probability of breakage represents in an increased probability of dispersal, and, if dispersal is sufficiently advantageous, a selection pressure could work 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.

d. *An Acorn Barnacle* - *S. cariosus*: An individual *S. cariosus* of the maximum size observed on Tatoosh Island has only an approximately 6% greater chance of surival than an individual twice this size (Figure 13d). In this case the mechanical factors described here clearly do not play as important role in size limitation.

e. *Limpets* - *C. digitalis*, *C. pelta*, *N. scutum*: The survivorship curves for the three limpet species are shown in Figure 14. The adhesive tenacity of stationary limpets of all three species is so great that mechanical limitation to size does not seem feasible (Figures 14aii, bii, cii). The decrease in tenacity accompaying locomotion, however, leads to another picture (Figures 14ai, bi, ci). 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 is plotted against number of waves rather than months. For all three species, after only a few waves a survivorship ratio of at least eight is reached between the maximum observed size and twice this size. For example, after 50 waves the 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 8 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. For limpets there is a large risk associated with movement. The smaller the limpet the less this risk, and 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 feasible.

The general picture emerging from the approximate survivorship curves presented here is one of size limitation through catastrophe. Where survivorship is high at the end of a year (> 0.90) survivorship ratios are necessarily low (i.e. *S. cariosus*, *M. californianus* end-on). Conversely, where survivorship is low (< 0.10) survivorship ratios exceed the value of eight required to invoke a selection pressure for smaller size. Thus, if the mechanical limits to size proposed here are operative in nature, they will have their most profound effect under conditions where within one reproductive cycle a large proportion of a population is dislodged. A winter with exceptionally rough storms would constitute such a condition for many species. Alternatively, such conditions could apply annually to an organism with a short maturation time, one which matures during summer's calm seas but may be ravaged by an early fall storm (e.g. *Postelsia palmaeformis*).

Further, the survivorship curves presented here suggest an approximate "critical value" for $L d P_d/dL$. The two examples in which survivorship ratio at the end of a year is less than eight (*S. cariosus*, *M. californianus* end-on) have LdP_d/dL values less than 0.10 at the maximum size observed in nature. In all cases where the survivorship ratio exceeds 8 at the end of a year LdP_d/dL exceeds 0.10. It is on this basis that we have chosen 0.10 as the cut-off value for designating LdP_d/dL as "large" or "small". This value is intended only to be 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.

The examples cited above 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 mechanical factors alone may form 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 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, there are several aspects of the flow forces associated with waves for which the model does not account, 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 $\underline{F_{df}}$ 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 (eg. 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 a limpets. However, for other species in other habitat this assumption is clearly violated, mussels being a good example. The mussel tenacities measured in this study were taken from solitary mussels, which are occasionally found on Tatoosh Island, and thus are appropriate for the calculations made above. However, the vast majority of mussels on Pacific Northwest shores do not occur as solitary individuals, but instead form large, tightly-packed beds (Paine and Levin 1981). Although hydrodynamic forces may be important in limiting the sizes of organisms in aggregations, as will be discussed below, these forces are not appropriately described by the model presented here.

3. The model presented here assumes that the coefficients $\underline{C_d}$, $\underline{C_m}$, and $\underline{C_l}$ are constant for a given body shape. In at least the case of $\underline{C_d}$, the drag coefficient, this is a gross oversimplification; $\underline{C_d}$ clearly varies as a function of Reynolds number, $\underline{Re}$, (Figure 1) and, for a given set of flow parameters, is thus itself a function of size. The dependence of the inertia coefficient, $\underline{C_m}$, and the lift coefficient, $\underline{C_l}$, on $\underline{Re}$ is less clear, as is the dependence all of

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 approximately 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, a cylinder with surface roughness elements of height only 1% of the diameter has a C_d decreasing only from 1.2 to approximately 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. The most smooth and regularly shaped organisms dealt with here, limpets, have a C_d decreasing only from approximately 0.7 to 0.5 over a tenfold 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 in C_d with K has not been studied for biological objects. However, Sarpkaya and Tuter (1974) have shown that at Re of 5.10^4 to 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 shapes near surfaces are those presented in Figure 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 in 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" (i.e. inviscid) flow, theory proclaims that C_m is a constant for a given shape, regardless of size (Batchelor 1967). The method by which C_m values were measured here minimizes the "non-ideal" aspects of the flow by measuring C_m at very low velocities; and the measurements are thus close to those predicted by theory (Daniel, 1982). 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) have shown for spheres and cylinders that for K greater than approximately 20 (the range of interest here) C_m does not vary substantially. Sarpkaya and Tuter (1974) also show that C_m increases as the Re increases in the range from Re = $10^4 - 10^6$. If these results hold true for biological objects near a solid boundary it is quite possible that C_m values higher than those used in the above calculations are present. Further research will be necessary to resolve this possibility.

We speculate, then, that when a full knowledge of the variation in C_d,C_l, and C_m is available the C_d values used here will be overestimates, the C_l values approximately correct, and the C_m values, underestimates. The net result of a model corrected for the size-dependent variation in coefficients would be in each case to: 1) lower the estimate of the size independent probability of dislodgement and 2) increase the $L\ dP_d/dL$. Thus, if our speculation about the size-dependence of C_d, C_m, and C_l proves true, our argument for the role of water acceleration in size limitation will 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 here

using actual breaking stress measurements which themselves contain some experimental error. Unless these experimental errors are strongly biased (e.g. the basal area of small barnacles is overestimated while that of large barnacles is underestimated), and all reasonable precautions were taken to preclude such biases, the experimental errors serve to increase the apparent variance of the breaking stress distribution. From an examination of equation 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 the argument made here for the role of acceleration in size limitation.

5. The model proposed here 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 available concerning this point 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 will 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. There are a number of plants and animals on surf-beaten shores with features that permit them to attain sizes larger than our model would predict. Among the mechanisms permitting large size are 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 (e.g., Delf 1932, Koehl and Wainwright 1977, Koehl 1979), and corals (e.g., Wainwright et al. 1976, Vosburgh 1977, 1982, Chamberlain 1978, this study) fall within 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. When dislodging plants or animals, it was found that in many cases 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, 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. palmaefornis). Furthermore, on many wave-swept shores space is a limited resource (see for example, 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. Because organisms in aggregations can be shielded by their neighbors, they can be in microhabitats exposed to much lower flow velocities and accelerations than those characterizing mainstream flow at a site

(Wainwright and Koehl 1976; Koehl 1977a, 1977b). 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 (e.g., 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 (eg. Pollicipes polymerus), a more useful approach might be to apply the model to the entire clump rather than to individuals within it.

While considering possible mechanical limits to size, note that 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). The difference in magnitude between the mechanical stresses experienced by the large and small organisms in this case would be even greater than our predictions, which were made assuming 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).

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.

Mobile animals, such as snails, can move into protected microhabitats on wave-beaten shores. As mentioned above, the size of such refuges may in some cases impose an upper limit on the sizes these animals can attain (e.g., Kohn 1971, Emson and Faller-Fritsch 1976).

Flexible organisms such as seaweeds on wave-swept shores can attain relatively large size. For example, macroalgae such as *Lessoniopsis littoralis* in the low intertidal zone on Tatoosh Island can reach lengths (stipe plus blades) greater than 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 such 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, in press). 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 acceleration is lower than those of more spherical bodies, which in turn are lower than the C_m's of flattened bodies normal to the acceleration (Daniel 1983). Furthermore, if a tall flexible organism is surrounded by other organisms or is thin (i.e. 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 an organisms in waves) can be damped out by bendable, soft, or stretchable bodies (see 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: rigid, brittle organisms such as stony corals suffered more breakage than did flexible, deformable organisms like gorgonians (Woodley et al. 1981). Nonetheless, we should also point out that in certain cases, flexiblity 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 (e.g. Hoerner 1965). Furthermore, if structures are flexible enough to oscillate in waves, they can perish by fatigue fracture (e.g. Weigel 1972). The behavior of flexible organisms in waves is a complex mechanical problem that merits further analysis.

The heaviest wave action generally accompanies seasonal storms (e.g. Schwenke 1971, Harger 1972, Menge 1972, Paine and Levin 1981) or isolated events like hurricanes and typhoons (e.g. Stoddart 1962, 1963, Endean 1976, Randall and Eldridge 1977, Smith and Harrison 1977, Vosburgh 1977, Woodley, et al., 1981, Highsmith 1982). Some sessile organisms (e.g., certain algae and colonial invertebrates) that grow "too large" during non-stormy intervals are pruned to a smaller size during periods of heavy wave action rather than being completely ripped off the substratum. The places at which 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 in 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 can the stump survive, but so can broken-off fragments. "Programmed fragmentation" of this sort has been proposed as a mechanism of assexual reproduction and dispersal for many corals (e.g., 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 (Santilices et al. 1980).

To this point we have dealt solely with mechanical limits to size, and have treated large size as if it were an unquestioned "good thing", i.e. advantageous to the organism. This is not necessarily so, and in order to place the ideas proposed here in a context that will be useful in the examination of real wave-swept communities, we briefly examine 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. A number of advantages to large size have been suggested:

Large individuals are better able to ward off some types of pedators than are small individuals (e.g. Gould 1966, Connell 1970a, 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, and a number of other studies 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 surface area to volume ratio than do smaller creatures, the large organisms are better insulated from fluctuations in external conditions and can regulate their internal environment more easily (Gould 1966, Stanley 1973). Many organisms exposed to wave action are intertidal and thus are often exposed to drying in air and/or heating in the sun. That large intertidal organisms survive exposure to air longer than do smaller members of the same species has been demonstrated (e.g. Johnson and Shick 1977). Although sessile individuals must survive being small in the same spot that they occupy when large (Paine 1981), daytime low spring tides during warm sunny weather are seasonal occurrences at many sites - an organism at such a site could conceivably settle and 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 water-borne 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 to suffer some damage by projectiles than are small ones (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). Conversely, 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 repoductive 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 catagories 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). As Armstrong (1977) has pointed out, large organisms that can take big food items may have a competitive advantage over small ones when the food resource distribution is skewed towards large size.

Large organisms are more efficient metabolically (i.e. have a lower metabolic rate per unit body mass) than small organisms (e.g. 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, 1970b, Paine 1966, 1981, Palmer 1980), and may thus remove the big individuals from a population. If a particular type of organism must hide (from dessication, waves, or predators, for example), the sizes of refuges available at a particular site may limit the maximum sizes of the organisms (e.g., 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 (e.g., Ebert 1968).

The size, and thereby 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, 1976a; 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 (Seed 1969, Sutherland 1970, Connell 1961a, 1972, 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). Note that a few intertidal species show the opposite trend in size distribution (i.e., larger individuals higher on the shore)(e.g., 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 oganisms 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 the proposed here be usefully applied?

Our analysis provides a quantitative method for deciding whether wave forces alone may 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. If these values are high, it is possible that the size of that species is limited at that site by the wave forces encountered, and further, experimental efforts may be taken to confirm or refute this conclusion. In such a case where P_d and $L\, dP_d/dL$ are high, an examination *solely* of the possible *biological* factors limiting size would be ill-advised. Conversely if P_d and $L\, dP_d/dL$ are low, wave forces may reasonably be discounted and further efforts focused on the role of biological interactions.

Even in those cases where wave forces may be 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. The hypothesis proposed here provides a mechanism whereby larger organisms are exposed to a greater probability of death. This size-specific mortality could conceivably serve to decrease the size at which an organism optimizes its intrinsic rate of increase (sensu Roff 1981) and could thereby affect selection for smaller individuals.

Alexander (1981) has outlined a theory whereby the safety factors with which biological structures are constructed can be predicted. Data collected from examination of animal structure in regards to 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 present in a given habitat. 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.

The ideas proposed here, by quantifying the "exposure" (_ie._ the 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 (e.g., Levin and Paine 1974, 1975, Paine and Levin 1981, Connell and Slayter 1977, Connell 1978, Sousa 1979a, 1979b, Quinn 1979, and many others cited therein). 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 to 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 periods of heavy wave action at a site, should be of basic importance in the dynamics of the community (e.g., Paine and Levin 1981).

Size-dependent predation can have important effects on population and community structure (e.g., 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 (e.g., 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.

SUMMARY

1. There are many advantages to large size.
2. Despite these advantages most wave-swept organisms are small.
3. The accelerational component of flow in breaking waves places a size-

dependent mechanical stress on wave-swept organisms. This size-dependent stress is hypothesized to be a limiting factor in the size to which many wave-swept organisms grow.

4. This hypothesis is tested using various intertidal species, and is conjectured to be valid for the limpets, *C. pelta* and *N. scutum*, the urchin, *S. purpuratus*, the mussel, *M. californianus* (when solitary), and the hydrocoral, *M. complanata*. For the snails discussed (*T. emarginata*, *T. canaliculata*, and *L. scutulata*) the mechanical environment poses an indirect constraint on body size and feeding behavior. For the acorn barnacle, *S. cariosus*, mechanical limits appear to be less of a factor in limiting size.

5. A definitve answer regarding the possibility of mechanical limitations to size depends on factors that remain to be measured: long-term wave force probabilities, and life history parameters.

6. Flexibility, posturing, pruning, and life cycle strategies provide possible mechanisms for circumventing the size limitations due to acceleration.

7. The hypothesis proposed here may prove useful in examining the ecology of wave-swept communities by providing a quantitative means for measuring the importance of mechanical factors in the functioning of organisms.

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APPENDIX 1

Symbol	Definition	Units	Eq. where first used
A_b	Basal area of model or organism	m^2	20
A_c	Critical area	m^2	2
A_p	Projected area (direction of flow)	m^2	1
$A_{p,max}$	Maximum projected area	m^2	42
$A_{p,min}$	Minimum projected area	m^2	42
B	Proportionality constant	—	3
C_d	Drag coefficient	—	7
C_l	Lift coefficient	—	8
C_m	Added mass coefficient	—	6
C_p	Center of pressure	—	11
D	Specimen length (coral)	m	13
d	Distance from neutral axis	m	23
F	Loading force	N	13
F_a	Acceleration reaction	N	4
F_d	Drag force	N	1
F_{df}	Total force in direction of flow	N	4
F_l	Lift Force	N	8
g	Acceleration due to gravity	m/s^2	14
H	Wave height	m	14
H_{rms}	Root-mean square wave height	m	46
H_i	Pressure head at port i	m	11
I	Second moment of area	m^4	13

K	Proportionality constant	—	22
K	Period parameter	—	10
L	Characteristic length	m	5
L_h	Height of coral blade	m	28
L_r	Radius of animal or model	m	18
$L_{r,max}$	Maximum radius	m	26
m	Mass	kg	12
M	Moment (force x distance)	Nm	23
N	Number of waves encountered	—	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
$P_{(H>H')}$	Probability that a wave has a height > H'	—	46
P_s	Probability of survival	—	30
$P_{s,cum}$	Cumulative probability of survival	—	31
P_U	Probability of encountering velocity U	—	44
P_{U_i}	Probability of encountering velocity in range U_i	—	48
$P(U>U')$	Probability that a wave has a velocity > U'	—	47
r_i	Radial distance to port i	m	11
Re	Reynolds number	—	9
s	Standard deviation of breaking stress	N/m^2	30

t	Time	s	14
T	Relative thickness (of coral blade)	—	28
T	Period of oscillation	s	10
U	Water velocity	m/s	1
U_m	Maximum water velocity in oscillatory flow	m/s	10
V	Volume of displaced fluid	m^3	4
y	Distance from neutral axis	m	13
W	Relative width (of coral blade)	m	28
x	Distance from leading edge	m	15
Z	Water depth	m	14
α	Angle relative to mainstream velocity	degrees	11
α	Added mass coefficient	—	12
δ	Boundary layer height	m	15
ν	Kinematic viscosity of water	m^2/s	9
ϕ	Cone angle	degrees	11
ρ	Density of water	kg/m^3	6
σ	Stress (force/area)	N/m^2	2
$\bar{\sigma}$	Average breaking stress	N/m^2	30
$\sigma_{eq,max}$	Equivalent maximum stress	N/m^2	42
σ_n	Normal stress	N/m^2	23
$\sigma_{n,max}$	Maximum normal stress	N/m^2	24
$\sigma_{s,max}$	Maximum shear stress	N/m^2	21

APPENDIX 2

Any change in the constants or coefficients appearing in eqs. 30 and 31 causes the estimate of maximum size to vary. The relative sensitivity of $L_{r,max}$ to variations in C_d, C_m, C_l, U, σ_{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

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

For small errors such that

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

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

etc. for $\underline{C_d}$, $\underline{C_m}$, $\underline{U}$, and $d\underline{U}/d\underline{t}$

we may linearize the above equation as:

$$\begin{aligned}\Delta \underline{L_{r,max}} = {} & [\partial \underline{L_{r,max}}/\partial \sigma_{\underline{s,max}}]\Delta \sigma_{\underline{s,max}} \\ & + [\partial \underline{L_{r,max}}/\partial \underline{C_d}]\ \Delta \underline{C_d} \\ & + [\partial \underline{L_{r,max}}/\partial \underline{C_m}]\ \Delta \underline{C_m} \\ & + [\partial \underline{L_{r,max}}/\partial \underline{U}]\ \Delta \underline{U} \\ & + [\partial \underline{L_{r,max}}/\partial d\underline{U}/d\underline{t}]\ \Delta d\underline{U}/d\underline{t}\ .\end{aligned}$$

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

$$\begin{aligned}\Delta \underline{L_{r,max}}/\underline{L_{r,max}} = {} & [\partial \underline{L_{r,max}}/\partial \sigma_{\underline{s,max}}]\ [\Delta \sigma_{\underline{s,max}}/\underline{L_{r,max}}] \\ & + [\partial \underline{L_{r,max}}/\partial \underline{C_d}]\ [\Delta \underline{C_d}/\underline{L_{r,max}}] \\ & + [\partial \underline{L_{r,max}}/\partial \underline{C_m}]\ [\Delta \underline{C_m}/\underline{L_{r,max}}] \\ & + [\partial \underline{L_{r,max}}/\partial \underline{U}]\ [\Delta \underline{U}/\underline{L_{r,max}}] \\ & + [\partial \underline{L_{r,max}}/\partial d\underline{U}/d\underline{t}]\ [\Delta d\underline{U}/d\underline{t}/\underline{L_{r,max}}]\end{aligned}$$

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

$$\begin{aligned}\Delta \underline{L_{r,max}}/\underline{L_{r,max}} = {} & \sigma_{\underline{s,max}}/A + [\underline{U}^2 \rho \Delta \underline{C_d}]/3A + [\rho\ \underline{C_d}\ \underline{U}\ \Delta \underline{U}]/3A \\ & + [\Delta d\underline{U}/d\underline{t}]/[d\underline{U}/d\underline{t}] + \Delta \underline{C_m}/\underline{C_m}\end{aligned}$$

Thus a 10% variation in $d\underline{U}/d\underline{t}$ or $\underline{C_m}$ will always produce a 10% variation in $\underline{L_{r,max}}$. In contrast, the relative variation in $\underline{L_{r,max}}$ caused by a 10% variation in $\sigma_{\underline{s,max}}$, $\underline{C_d}$, or $\underline{U}$ depends on the magnitude of $\sigma_{\underline{s,max}}$, $\underline{C_d}$, and $\underline{U}$. For example a 10% variation in $\underline{C_d}$ causes a 0.14% variation in $\underline{L_{r,max}}$ for a well streamlined organism with a very strong adhesive under severe flow conditions ($U = 20$ m/s, $C_d = 0.1$, $\sigma_{s,max}s = 10^6$ N/m^2). 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/m^2). A typical example from this study would be the limpet *C. digitalis* while moving in moderate to high flow ($U = 10$ m/s, $C_d = 0.525$, $\sigma_{s,max}$ 1.29×10^5 N/m^2) where a 10% variation in C_d would result in a 1.6% variation in $L_{r,max}$.

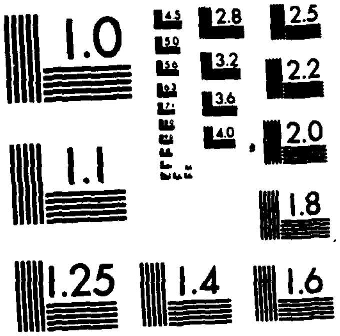
A similar sensitivity analysis can be carried out for eq. 27 and is presented here without derivation.

$$B \equiv [\,32/9\pi]\,\rho\, C_m\, dU/dt$$

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

AD-A134 709 MECHANICAL LIMITS TO SIZE IN WAVE-SWEPT ORGANISMS(U) 2/2
WASHINGTON UNIV SEATTLE DEPT OF ZOOLOGY
M W DENNY ET AL. 10 NOV 83 N00014-79-C-0611

UNCLASSIFIED F/G 8/1 NL



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A

TABLE 1.

Adhesive tenacity values and hydrodynamic parameters for a variety of Wave-swept organisms

SPECIES	shear strength (N/m^2 x 10^5)	standard deviation	tensile strength (N/m^2 x 10^5)	standard deviation	$\overline{C_d}$, drag coefficient.	$\overline{C_l}$, lift coefficient	α, added mass coefficient
LIMPETS							
Collisella digitalis (s)	3.85	1.75			0.52	0.25	0.84
Collisella digitalis (m)*	1.29	0.91			0.52	0.25	0.84
Collisella pelta (s)			2.05	0.93	0.45	0.47	0.68
Collisella pelta (m)*			0.69	0.48	0.45	0.47	0.68
Notoacmaea scutum (s)			1.73	0.79	0.45	0.47	0.68
Notoacmaea scutum (m)*			0.58	0.41	0.45	0.47	0.68
Patella vulgata[1] (s)			1.86	0.52			
Patella vulgata[1] (m)*			0.62	0.44			
Patella cochlear[2] (s)			5.18	0.94			
Patella cochlear[2] (m)*			1.73	1.22			
Patella argenvillei[2] (s)			4.67	0.80			
Patella argenvillei[2] (m)*			1.56	1.10			

TABLE 1. (cont.)

SPECIES	shear strength (N/m^2 x 10^5)	standard deviation	tensile strength (N/m^2 x 10^5)	standard deviation	$\underline{C_d}$, drag coefficient	$\underline{C_1}$, lift coefficient	α, added mass coefficient
LIMPETS (cont.)							
Patella longicosta^2 (s)			4.40	1.15			
Patella longicosta^2 (m)*			1.47	1.04			
Patella granularis^2 (s)			3.25	0.83			
Patella granularis^2 (m)*			1.07	0.77			
Patella granatina^2 (s)			2.71	0.84			
Patella granatina^2 (m)*			0.91	0.64			
Patella occulus^2 (s)			1.95	0.45			
Patella occulus^2 (m)*			0.65	0.46			
BARNACLES							
Semibalanus cariosus	3.29	1.70			0.52		0.31
Balanus glandula	4.17	2.31			0.52		0.73
Balanus nubilis	4.84	1.60			0.52		0.31

TABLE 1. (cont.)

SPECIES	shear strength (N/m^2 x 10^5)	standard deviation	tensile strength (N/m^2 x 10^5)	standard deviation	$\underline{C}_d$, drag coefficient	$\underline{C}_l$, lift coefficient	α, added mass coefficient
MUSSEL							
Mytilus californianus							
end-on	1.25^{+}	0.40			0.20		0.20
broadside	1.25^{+}	0.40			0.80		1.00
SNAILS							
Thais canaliculata^3 (s)	0.178‡	0.034			0.67$^{\#}$		0.72
Thais canaliculata^3 (m)	0.023	0.009			0.67		0.72
Thais emarginata^3 (s)	0.213	0.134			0.67		0.72
Thais emarginata^3 (m)	0.053	0.035			0.67		0.72
Littorina scutulata^3 (s)	0.310‡	0.080			0.67		0.72
Littorina scutulata^3 (m)	0.114	0.022			0.67		0.72

TABLE 1. (cont.)

SPECIES	shear strength (N/m^2 x 10^5)	standard deviation	tensile strength (N/m^2 x 10^5)	standard deviation	$\underline{C_d}$, drag coefficient	$\underline{C_l}$, lift coefficient	α, added mass coefficient
URCHIN							
Strongylocentrotus purpuratus	0.38	0.23			1.00	0.55	0.38
HYDROCORAL							
Millepora complanata			123	43	1.80		5.00

* moving values calculated as described in the text

1 Grenon and Walker 1982

2 Branch and Marsh 1978

3 Miller 1974

+ equivalent stress values (see text)

‡ values for shear calculates as same proportion of normal tenacity shown by *T. emarginata* (Miller 1974)

A.R. Palmer, pers. com.

TABLE 2. Shape constants for various standard shapes.

	Hemisphere	Cone	Cylinder
K_1	$(1/3)\ C_d$	$(2/3)B\ C_d$	$(4/3)B\ C_d$
K_2	$(8/9)\ C_m$	$(4/9)B\ C_m$	$(4/3)B\ C_m$
K_3	$(1/2)\ C_l$	$(1/2)\ C_l$	$(1/2)\ C_l$
K_4	$-.472\ C_l$	$-.472\ C_l$	$-.472\ C_l$
K_5	$(4/3\pi)\ C_d$	$(2-(2/[2]^{1/2})B^2 C_d$	$(2/\pi)B^2\ C_d$
K_6	$(32/9\pi)\ C_m$	$(4/3\pi)B^2\ C_m$	$2B^2\ C_m$

B = Height/radius

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

SPECIES	DIMENSION	LENGTH
Semibalanus cariosus	[illegible]	1.85×10^{-2}m
Balanus glandula	L_r	1.00×10^{-2}m
Balanus nubilis	L_r	4.75×10^{-2}m
Collisella digitalis	L_r	0.85×10^{-2}m
Collisella pelta	L_r	1.50×10^{-2}m
Notoacmaea scutum	L_r	1.50×10^{-2}m
Mytilus californianus	L	11.0×10^{-2}m
Stronglylocentrotus purpuratus	L_r	3.70×10^{-2}m
Millepora complanata	L_h	14.0×10^{-2}m
Thais emarginata	L	2.00×10^{-2}m
Thais canaliculata	L	2.00×10^{-2}m
Littorina scutulata	L	0.50×10^{-2}m

FIGURE LEGENDS

Figure 1. Drag and life coefficients (C_l and C_d) are plotted against log (Re) for a variety of organisms and standard shapes: acorn barnacle, *S. cariosus* (closed circles); limpet, *C. pelta* (open circles); hemisphere (open triangles); sphere (closed triangle). 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 measurd 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.

Figure 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 ports is placed at some angle, , 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 between each port and the underside of the cone.

Figure 3. Adhesive tenacity is plotted against shell length for the mussel *M. californianus*. The equation which describes these data is: Force = 1.65 x 10^4 L 1.95 where Force is expressed in N and L in m (r=0.86).

Figure 4. Volume is plotted against shell length for the mussel *M. californianus*. The equation which describes these data is: Volume = 0.061 L 2.86 where Volume is expressed in m^3 and L in m (r=0.98).

Figure 5. Water velocity (broken line) and acceleration (dashed line) during the initial portion of a typical wave, and the hydrodynamic force (solid line) they impose on an acorn barnacle are plotted against time.

Figure 6. 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 ($F_{df} \cdot b$) on the hemisphere. The lift force, F_l, imposes a moment ($F_{df} \cdot c$) 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.

Figure 7. Predictions for the urchin *S. purpuratus* exposed to a variety of water velocities (1,5,10, and 20 m/s). (a) Probability of dislodgment (P_d) is plotted against water acceleration ($L_{r,max}$ = 0.037 m). The size-specific increment in risk ($L\ dP/dL$) is plotted against size (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.

Figure 8. Predictions for the limpets *C. pelta* (a), *N. scutum* (b), and *C. digitalis* (c) exposed to a variety of water velocities (1 to 10 m/s). Predictions are based on adhesive tenacities for moving (solid lines) and statinary (dashed lines) limpets. Left panels: probability of dislodgement (P_d) is plotted against water acceleration for limpets of the observed maximum size ($L_{r,max}$). Righ panels: the size-specific increment in risk ($L\ dP_d/dL$) is plotted against size for limpets exposed to a water acceleration of 500 m/s^2. The observed maximum size is shown by a vertical broken line.

Figure 9. Predictions for the mussel, *M. californianus* exposed to variety of water velocities (1 to 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) is plotted against water acceleration for mussels of dimension L_{max}. Right panels: the size-specific increment in risk is 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.

Figure 10. Predictions for the fire coral, M. complanata exposed to a variety of water velocities (1 to 20 m/s). Left panel: the probability of breaking is plotted against water acceleration for a coral of blade length 0.14 m. Right panel: the size-specific increment in risk is 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.

Figure 11. Probability of dislodgement, (P_d) is plotted against water acceleration for stationary (left panels) and moveing (right panels) snails exposed to a variety of water velocities (1 to 20 m/s). (a) L. scutulata, 0.005 m in radius; (b) T. emarginata, 0.02 m in radius, (c) T. canaliculata, 0.02 m in radius. Notice that no animal can remain attached when exposed to a wave of 20 m/s.

Figure 12. Predictions for the barnacle, S. cariosus, exposed to water velocities of 1 and 20 m/s. Left panel: probability of dislodgement is plotted against acceleration for a barnacle 0.018 m in radius. Right panel: size-specific increment in risk is plotted against size (radius) for a barnacle exposed to a water acceleration of 500 m/s^2. The maximum radius observed is shown by the vertical dashed line.

Figure 13. The Log of the cumulative probability of survival ($P_{s,cum}$) is plotted against time (in months) for a variety of intertidal organisms. For each animal, predictions are calculated using: the maximum observed size (L), half that size (L/2), and twice that size (2L).

Figure 14. The log of the probability of survival is plotted against number of waves encountered while moving (left panels) and against time while stationary (right panels) for three limpet species: (a) C. pelta, (b) N. scutum, and (c) C. digitalis.

Fig 1

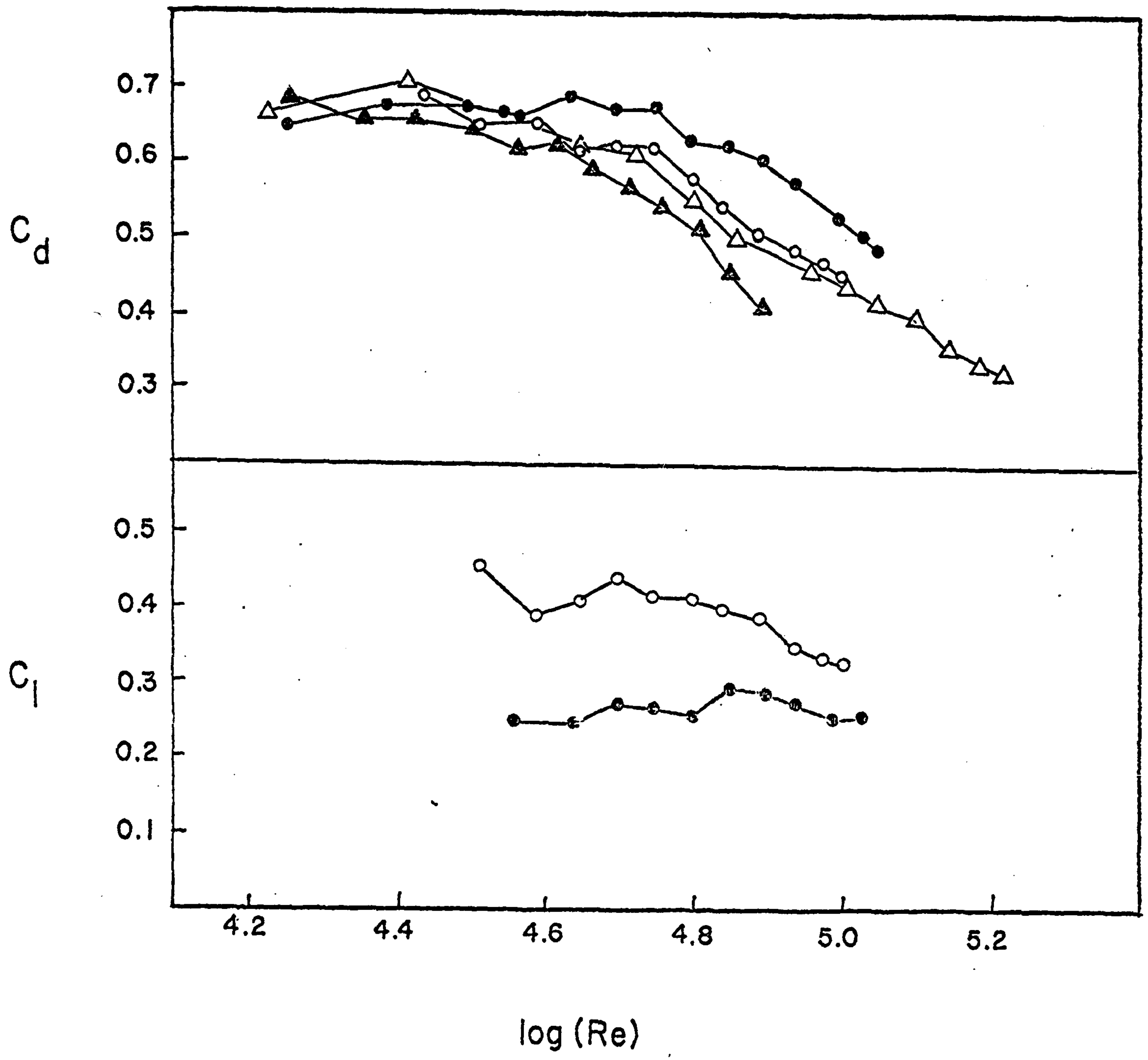


Fig 2

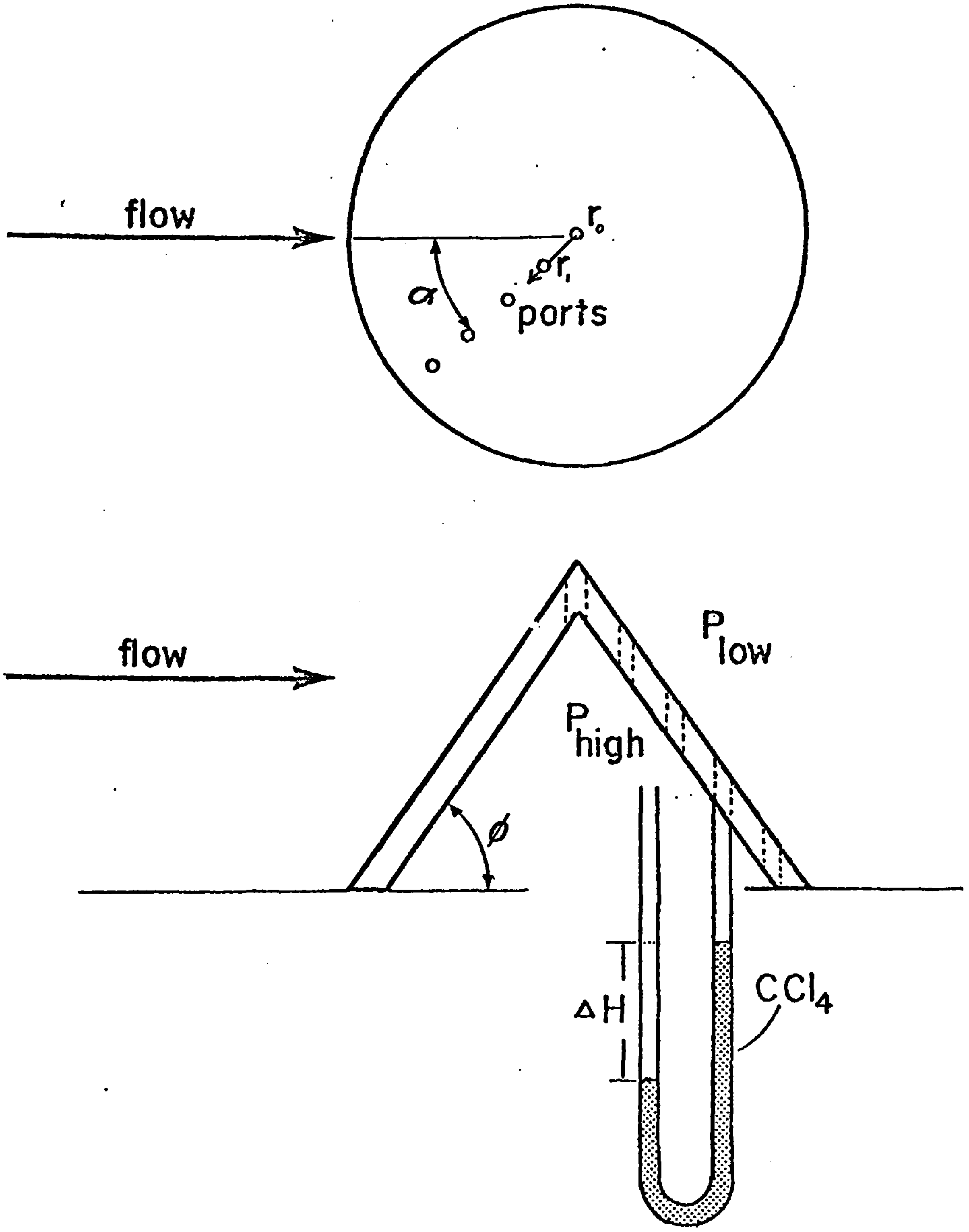


Fig 3

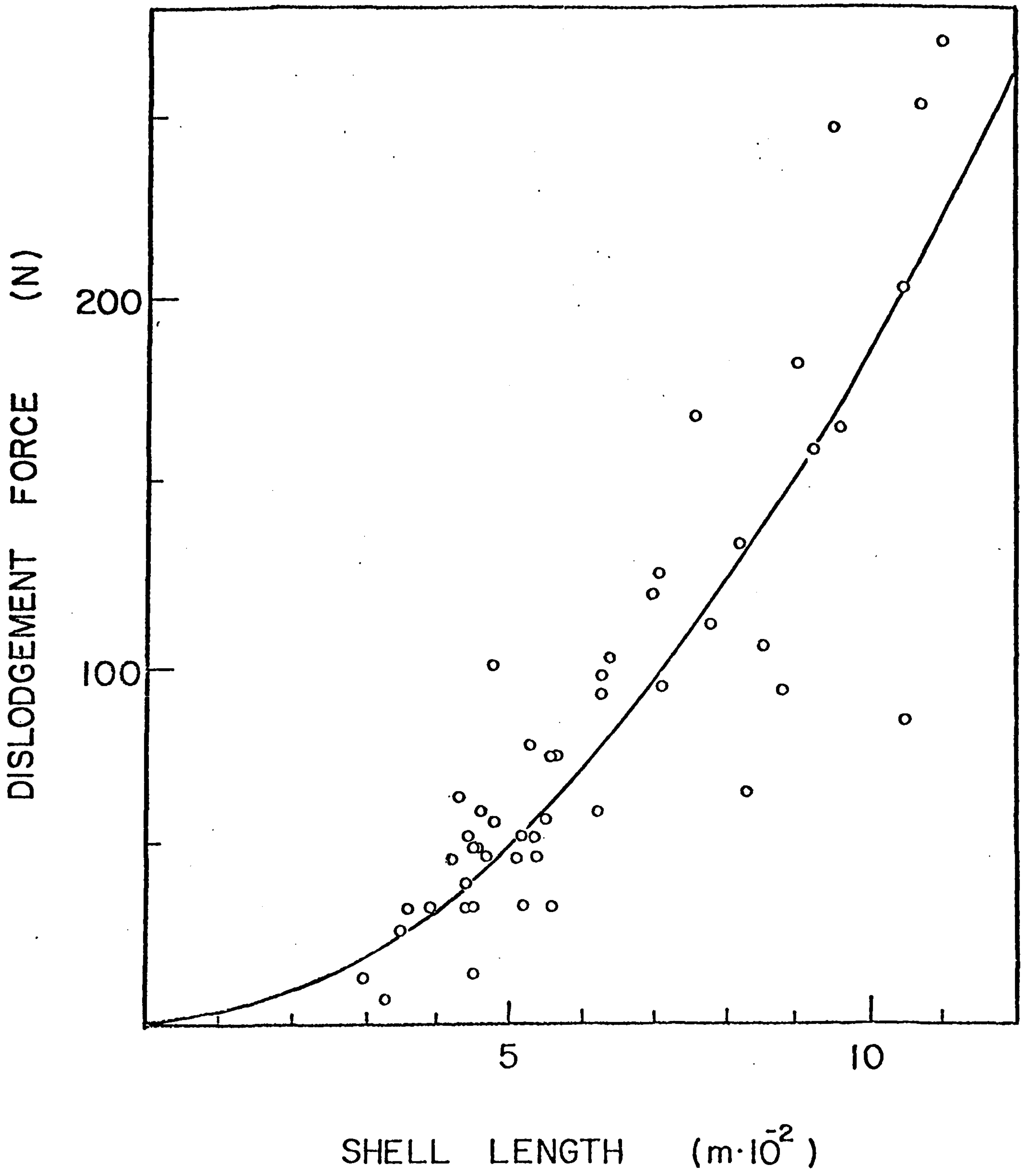
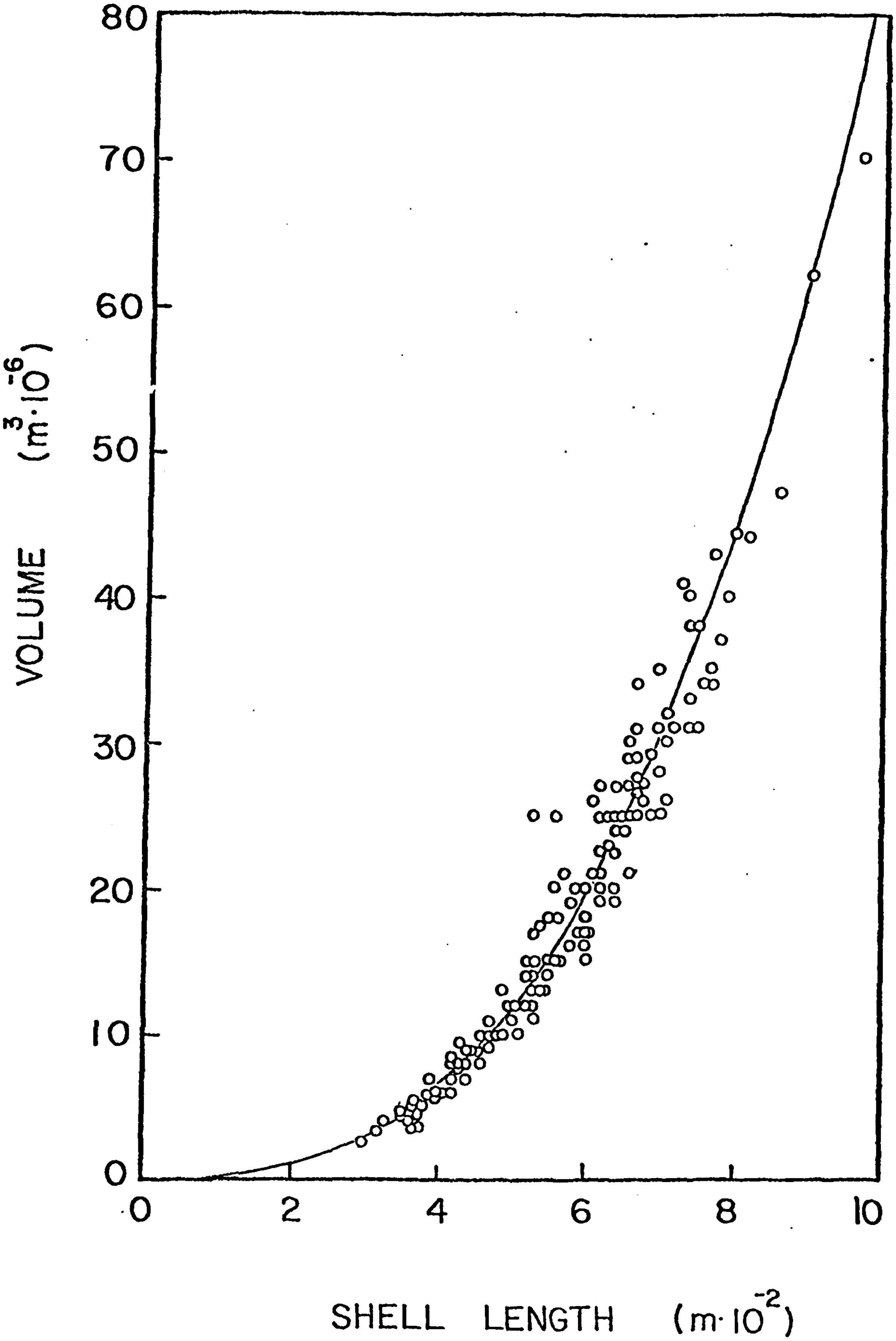


Fig 4



VOLUME $(m^3 \cdot 10^{-6})$
80
70
60
50
40
30
20
10
0
0
2
4
6
8
10
SHELL LENGTH $(m \cdot 10^{-2})$

Fig 5

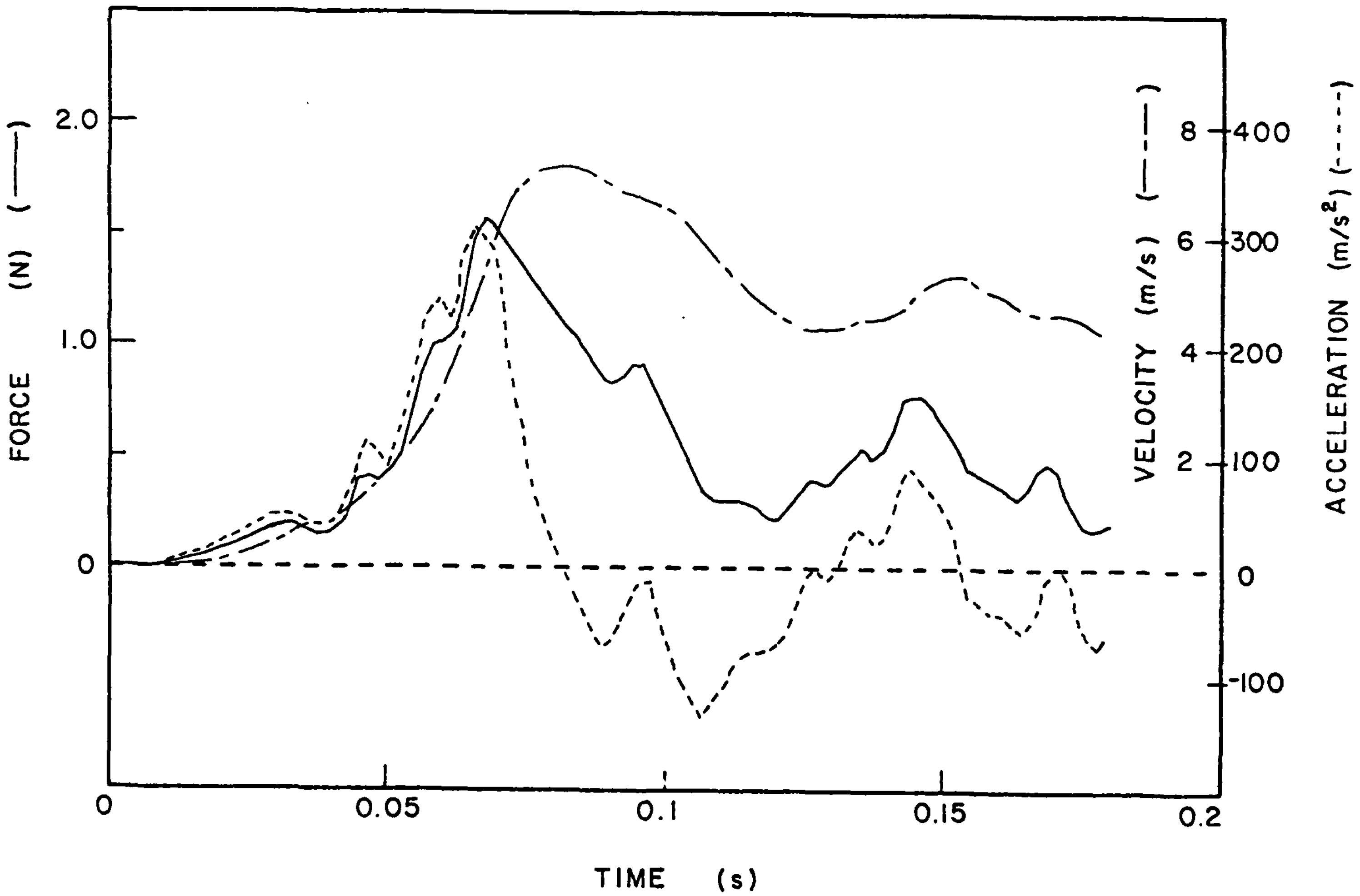

FORCE (N) (——)
2.0
1.0
0
VELOCITY (m/s) (— — —)
8
6
4
2
ACCELERATION (m/s²) (- - - - -)
400
300
200
100
0
-100
0
0.05
0.1
0.15
0.2
TIME (s)

Fig 6

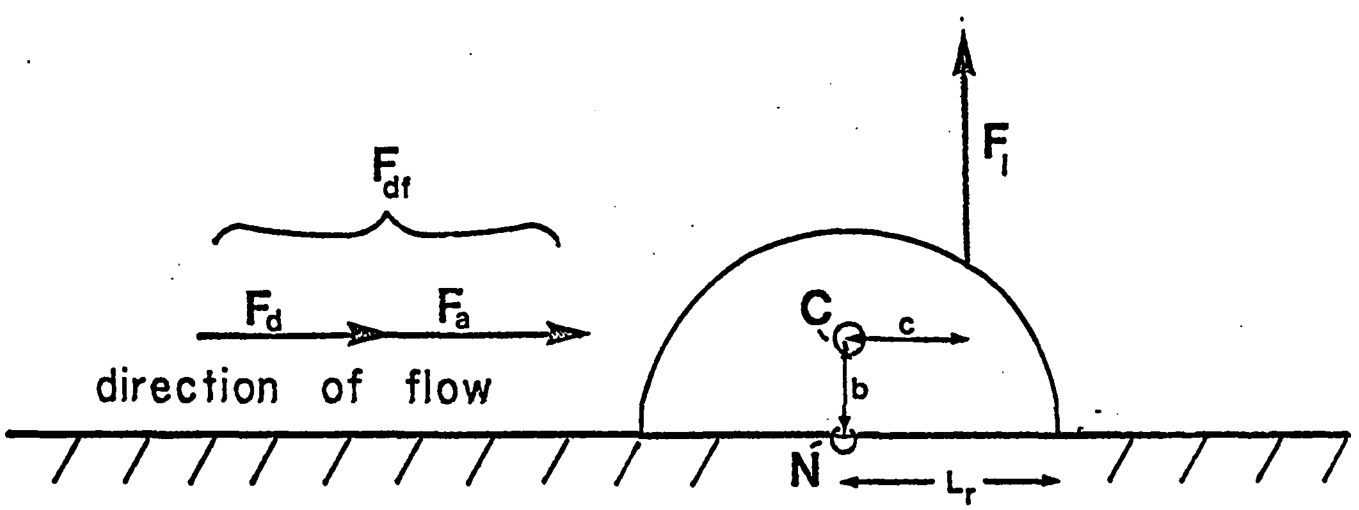


Fig 7

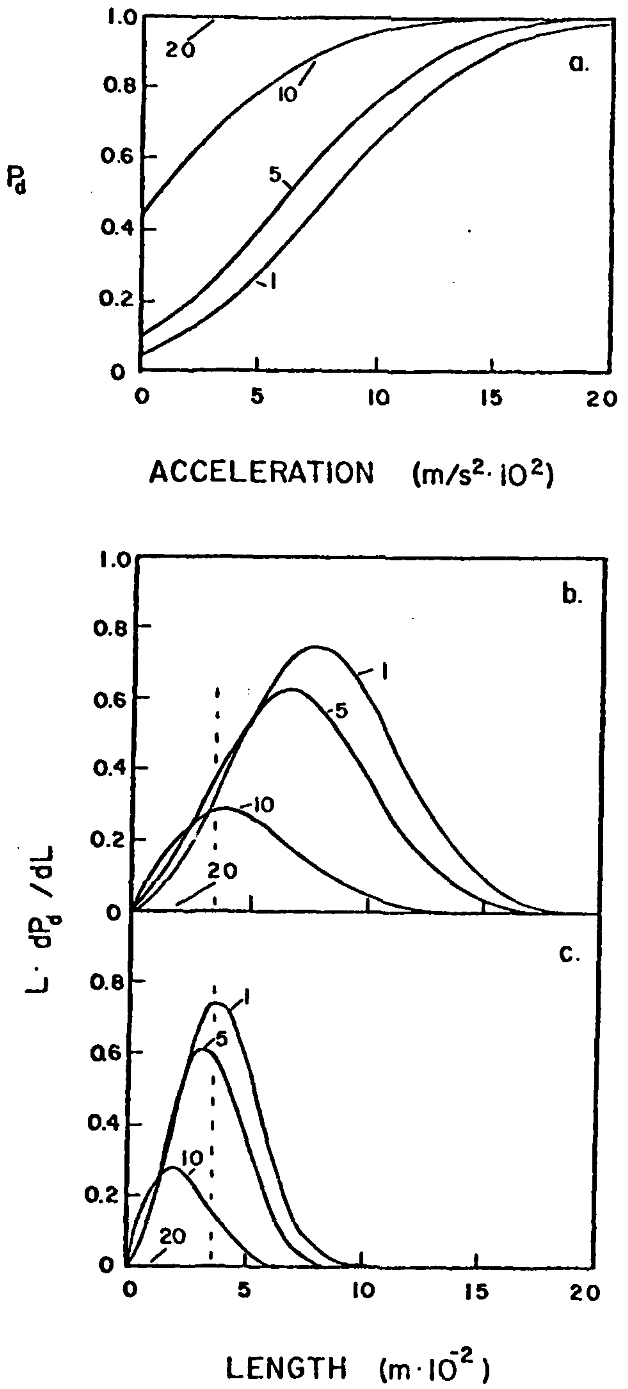
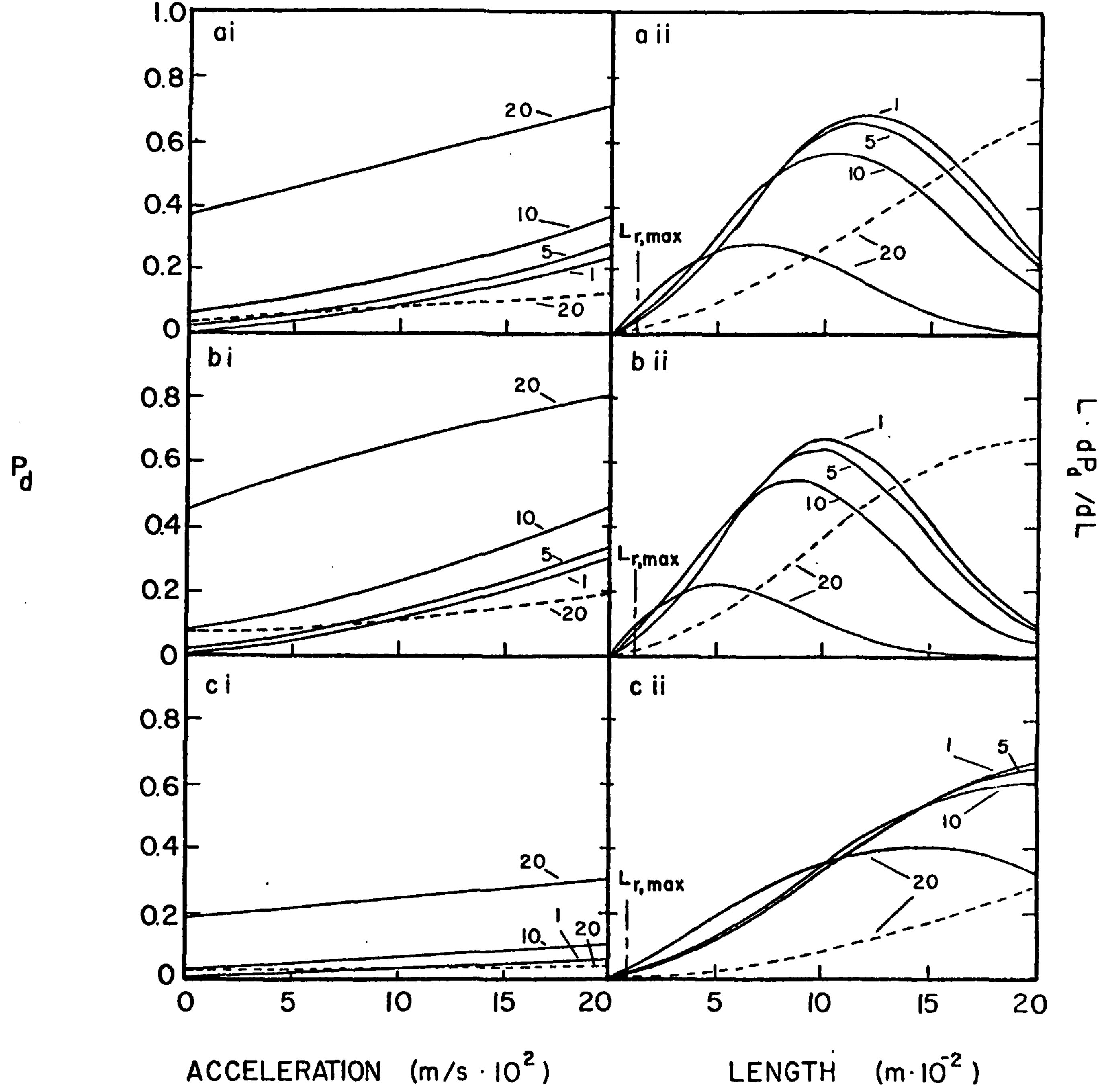
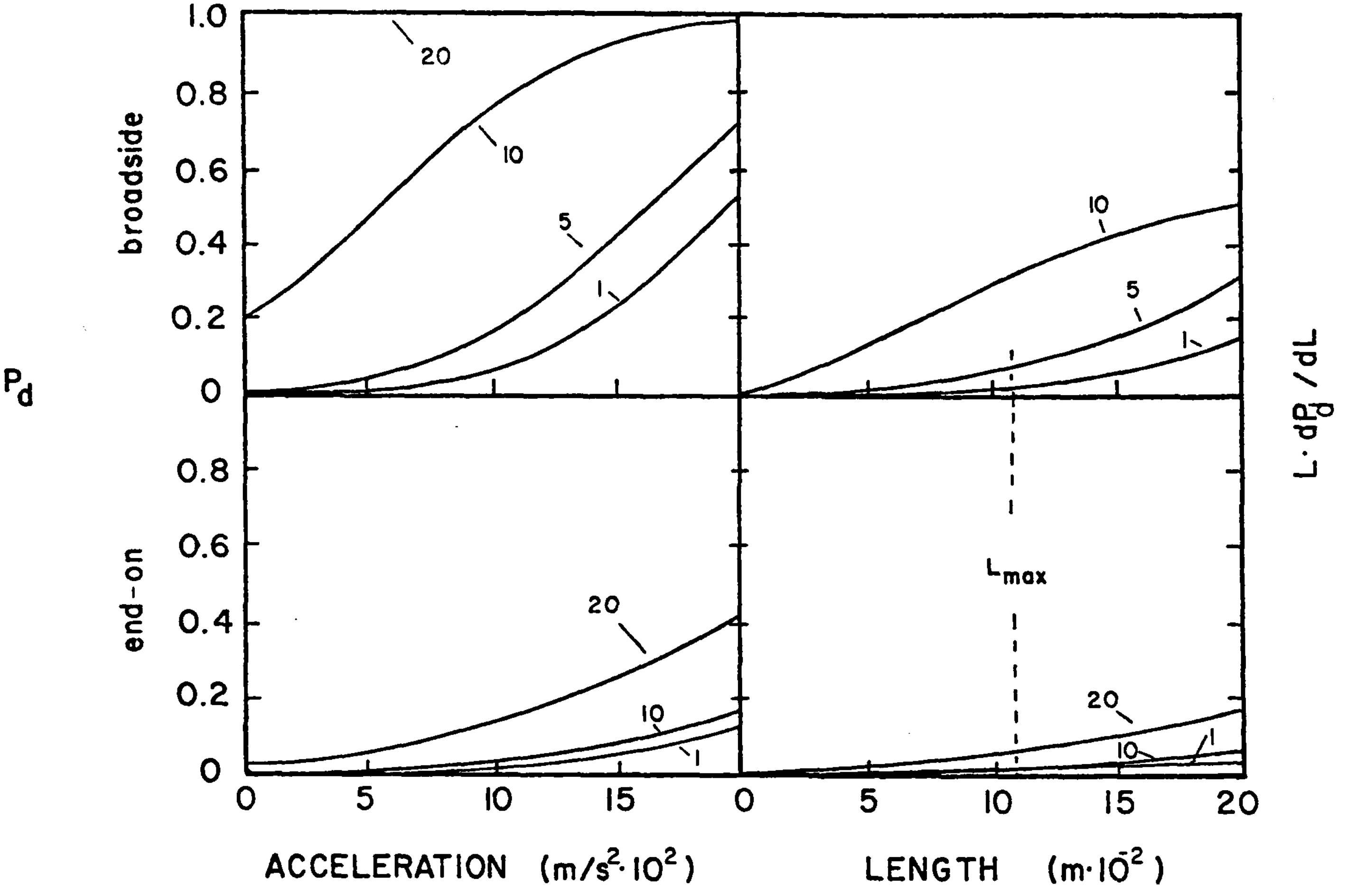

1.0
0.8
0.6
0.4
0.2
0
P_d
20
10
5
1
a.
0
5
10
15
20
ACCELERATION (m/s^2·10^2)
1.0
0.8
0.6
0.4
0.2
0
b.
1
5
10
20
$L \cdot dP_d/dL$
c.
0.8
0.6
0.4
0.2
0
1
5
10
20
0
5
10
15
20
LENGTH (m·10^{-2})

Fig 8



ai
a ii
bi
b ii
c i
c ii
P_d
L · dP_d /dL
L_r,max
20
10
5
1
1.0
0.8
0.6
0.4
0.2
0
5
15
ACCELERATION (m/s · 10^2)
LENGTH (m·10^-2)

Fig 9



P_d
broadside
end-on
1.0
0.8
0.6
0.4
0.2
0
0.8
0.6
0.4
0.2
0
20
10
5
1
20
10
1
0
5
10
15
ACCELERATION $(m/s^2 \cdot 10^2)$
10
5
1
L_{max}
20
10
1
0
5
10
15
20
LENGTH $(m \cdot 10^{-2})$
$L \cdot dP_d / dL$

Fig 10

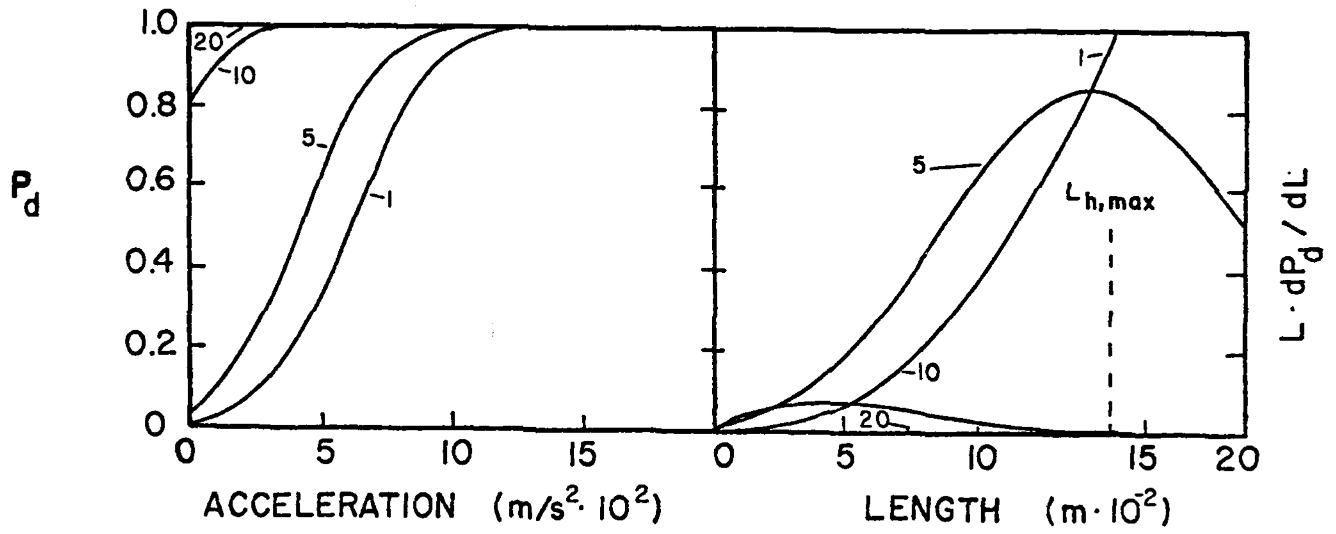

P_d
1.0
0.8
0.6
0.4
0.2
0
20
10
5
1
0
5
10
15
ACCELERATION $(m/s^2 \cdot 10^2)$
1
5
10
20
$L_{h,max}$
$L \cdot dP_d / dL$
0
5
10
15
20
LENGTH $(m \cdot 10^{-2})$

Fig 11

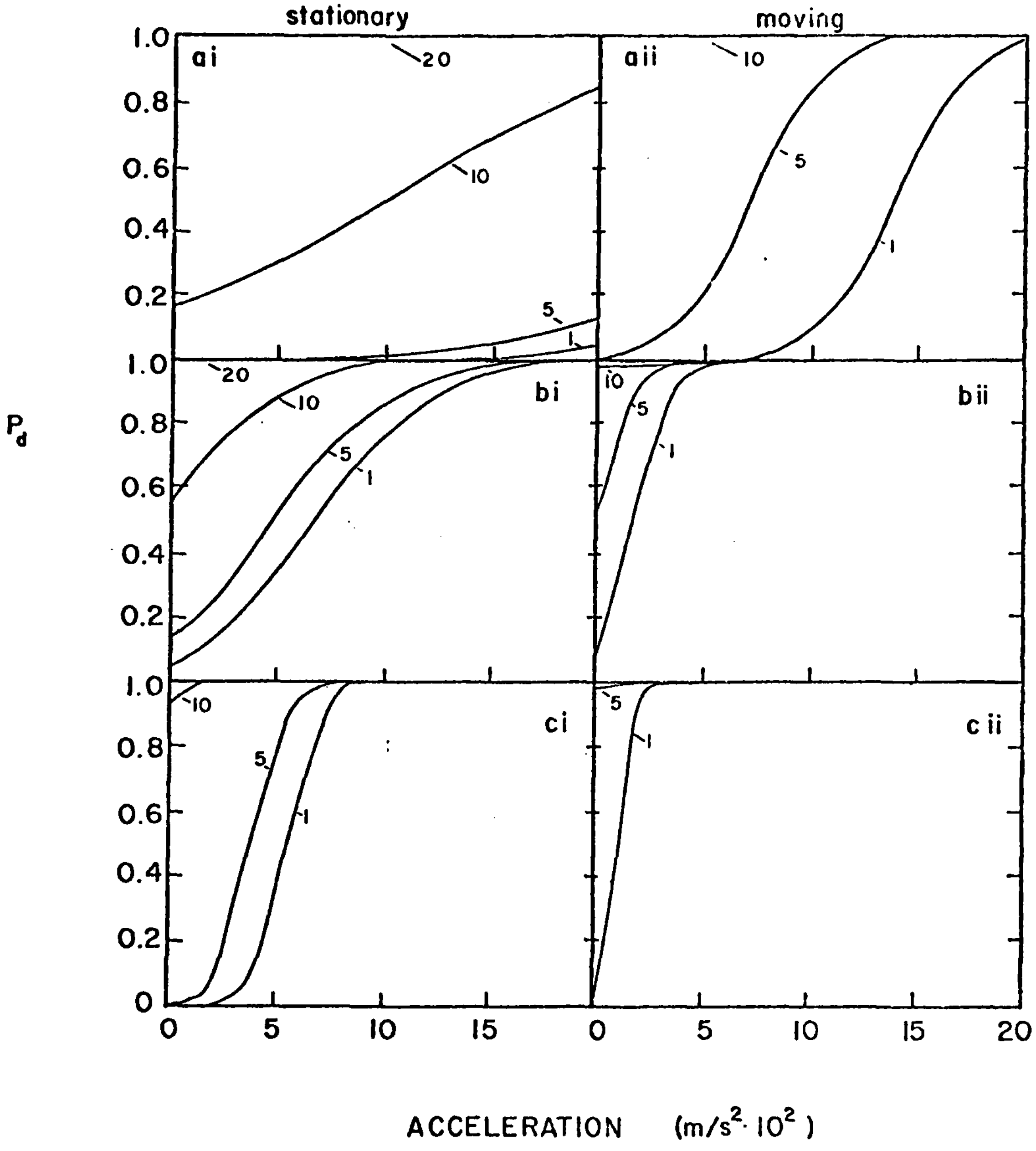

stationary
moving
ai
aii
bi
bii
ci
cii
20
10
5
1
Pd
1.0
0.8
0.6
0.4
0.2
0
0
5
10
15
20
ACCELERATION (m/s^2· 10^2)

Fig 12

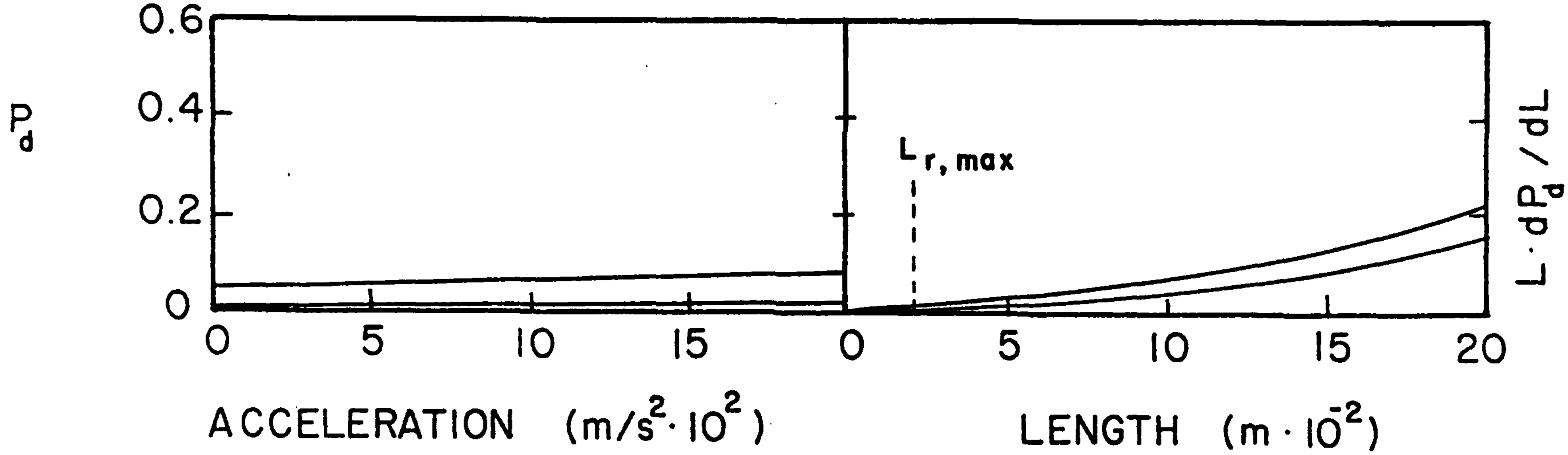

P_d
0.6
0.4
0.2
0
0
5
10
15
ACCELERATION $(m/s^2 \cdot 10^2)$
0
5
10
15
20
LENGTH $(m \cdot 10^{-2})$
$L_{r,max}$
$L \cdot dP_d / dL$

Fig 13

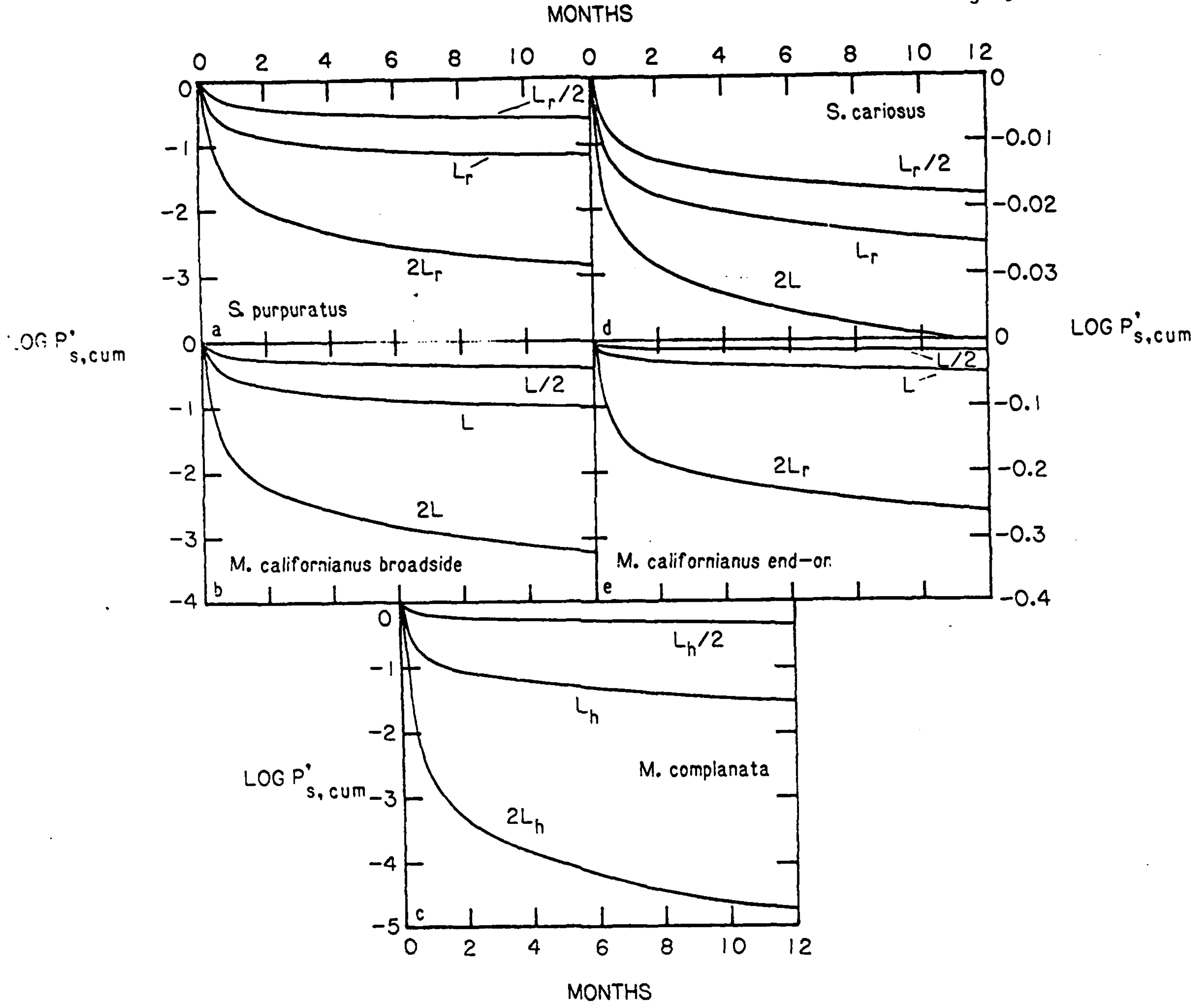
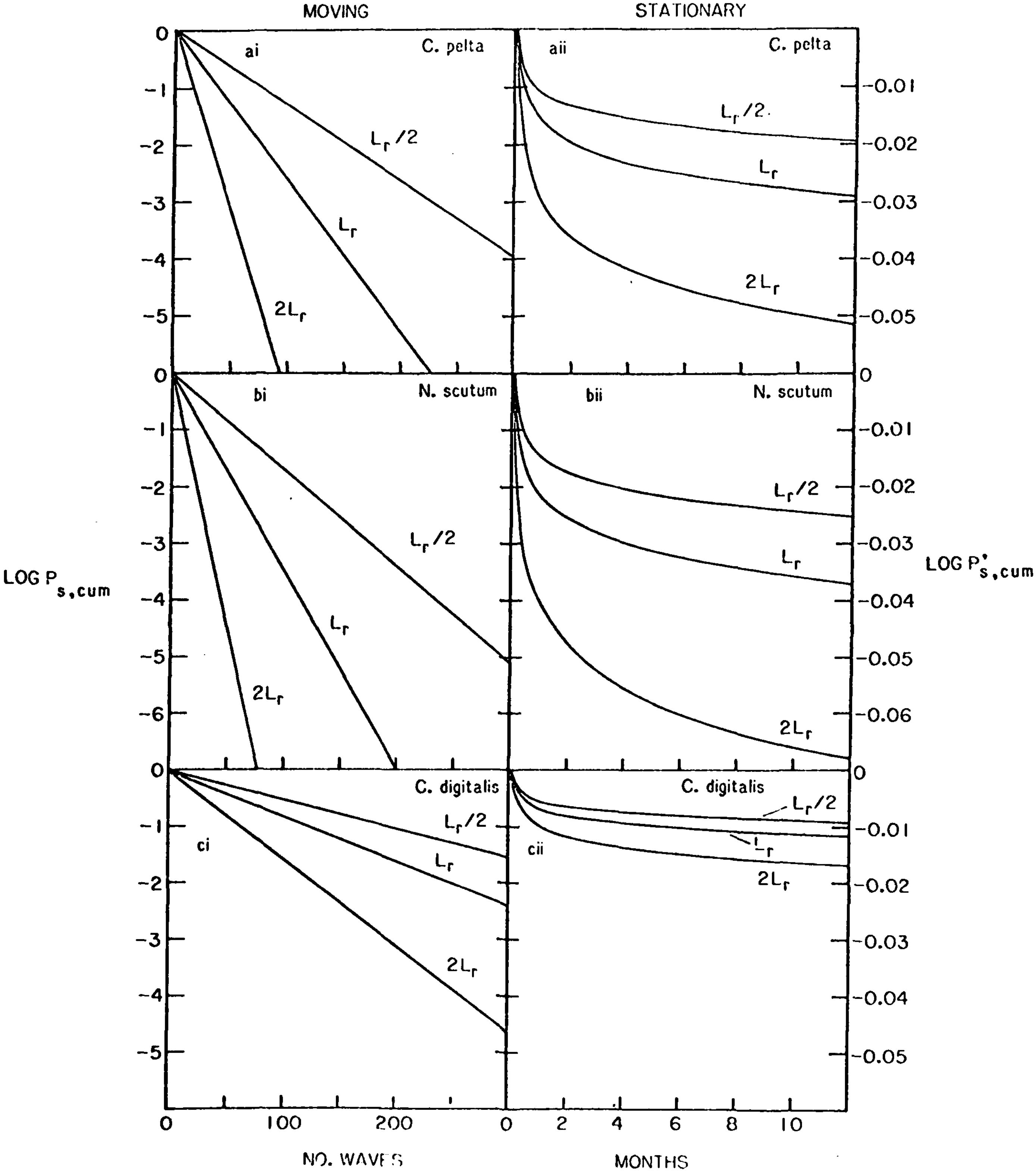

MONTHS
0
2
4
6
8
10
12
0
-1
-2
-3
-4
-5
0
-0.01
-0.02
-0.03
-0.1
-0.2
-0.3
-0.4
LOG $P'_{s,cum}$
LOG $P'_{s,cum}$
LOG $P'_{s,cum}$
a
S. purpuratus
$L_r/2$
L_r
$2L_r$
b
M. californianus broadside
L/2
L
2L
c
M. complanata
$L_h/2$
L_h
$2L_h$
d
S. cariosus
$L_r/2$
L_r
2L
e
M. californianus end-on
L/2
L
$2L_r$
MONTHS

Fig 14


MOVING
STATIONARY
ai
C. pelta
aii
C. pelta
L_r/2
L_r
2L_r
bi
N. scutum
bii
N. scutum
ci
C. digitalis
cii
C. digitalis
0
-1
-2
-3
-4
-5
-6
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
LOG P_s,cum
LOG P'_s,cum
0
100
200
0
2
4
6
8
10
NO. WAVES
MONTHS

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