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On the prediction of maximal intertidal wave forces

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Abstract

Understanding of the mechanics of "wave exposure" has been restricted by an inability to predict the maximal force encountered by particular wave-swept organisms on a time scale of months to years. In this study we attempt to remedy this situation by using the statistics of extremes to examine the hydrodynamic forces encountered by objects at a variety of intertidal sites. At each site a time series of wave-induced forces was divided into intervals, and the maximal force encountered in each interval was noted. Each maximum was normalized to the mean of the maxima for the series. The cumulative probability of encountering a given normalized force was found to be similar among objects and across a wide range of surf conditions and time scales. This observed cumulative probability distribution is consistent with that predicted from simple assumptions regarding the distribution of nearshore wave heights, the wave-height dependence of near-substratum water velocities, and the velocity dependence of hydrodynamic forces. The nature of this probability distribution allows one to predict on the basis of a relatively small number of measurements the maximal force a particular organism is likely to encounter in any given period. This information can in turn be used as a tool for exploring the ecological effects of disturbance and the evolution of body structure and life-history strategies.

Disturbance by wave-induced hydrodynamic forces can control the distribution and abundance of intertidal organisms. For example, the frequency with which boulders are overturned by waves can determine the course of succession on these rocky substrata (Sousa 1979a,b). The rate of patch formation in mussel beds—a rate controlled at least in part by the severity of wave action (Paine and Levin 1981; Denny 1987a)—can determine the local persistence of various algal species (Dayton 1971; Paine 1979; Sousa 1984). Many examples also demonstrate that the frequency and severity of physical disturbance can determine the diversity of species present at a given site (e.g. Connell 1978; Quinn 1979; Witman 1987).

The ecological implications of disturbance are dependent on the spatial and temporal patterns of disruption (*see* Sousa 1984, 1985). If the average time between disturbances (the return time) is less than the lifetime of major competitors in the system, the consequences of disturbance are different than if the return time is measured in many generations. The effects of distur-

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bance on life-history strategies are primarily consequences of the predictability of the disturbance or lack thereof (Sousa 1984, 1985).

Despite the biological importance of wave-induced physical disturbance, its physical basis has received little attention and is poorly understood. For example, at any given site it is not yet possible to predict a priori which organisms will be disturbed or how often. This inability to predict from an underlying mechanism the species-specific severity and return time of disturbance limits understanding of nearshore biology.

Two types of information are required to understand the mechanism of wave-induced disturbance. First, we need measurements of the hydrodynamic force required to "disturb" particular organisms. In many cases it is taken to be the force necessary to break or dislodge the plant or animal (e.g. Denny et al. 1985; Denny 1985, 1987a,b, 1988), but it could also be defined as the force required to prohibit foraging or reproduction. Data regarding strength and tenacity are available for a few wave-swept organisms (limpets: e.g. Branch and Marsh 1978; Denny et al. 1985; Denny 1985; mussels, barnacles, urchins: e.g. Denny et al. 1985; and corals: e.g. Chamberlain 1978; Tunnicliffe 1981; Vosburgh 1982), and there is no apparent practical problem in obtaining similar data for almost any wave-swept organism.

Second, we need measurements or accurate predictions of the maximal force exerted on organisms in a given period. To be most useful these measurements or predictions should refer to a period on the same order as the average time from settlement to last reproduction for the organism in question. In only a few cases have the hydrodynamic forces imposed on organisms by the wave-swept environment been directly measured (e.g. Koehl 1977; Denny 1982, 1983, 1985, 1987*a*; Denny et al. 1985) and for only a short period (a few tides at most). Practical problems with continuously measuring forces over periods approaching the potential lifetime of a plant or animal have proven restrictive. We are thus forced to extrapolate from short-term data to predict the maximal force that a plant or animal would encounter over its lifetime.

To date, these extrapolations have not met with much success. For example, Denny et al. (1985) noted that the drag and lift forces imposed on intertidal organisms are proportional to the square of the maximal water velocity which, for water at the crest of a breaking wave, is proportional to wave height (Carstens 1968). Therefore a knowledge of the temporal distribution of the heights of breaking waves potentially can be used as a basis for estimating maximal hydrodynamic forces. In making such predictions, Denny et al. (1985) relied on the assumption that inshore wave heights (and consequently the forces that they cause) follow a Rayleigh distribution. There are, however, two problems with this approach. First, the correspondence between wave height and the square of water velocity holds only when the crest of a breaking wave impinges directly on the organism in question (Carstens 1968; Denny 1988)-a situation that is probably rare. Second, waves near breaking deviate from a Rayleigh distribution of heights (Thornton and Guza 1983). These problems are reflected in the available data: Denny (1985, 1987a) noted that measured wave-induced forces exerted on limpets and mussels are not Rayleigh distributed.

Here we propose an alternative method for predicting maximal wave-induced forces. This method is based on the statistics of the extreme values encountered in a series of relatively short intervals and thereby avoids the necessity of knowing the precise underlying distribution of wave heights or water velocities. We demonstrate that forces encountered on wave-swept shores show a similar distribution of normalized extreme values for a variety of objects and over a wide range of surf conditions and time scales. This common distribution can be used in conjunction with simple, short-term force measurements to estimate the return time of forces of a specified magnitude, thereby providing a practical means by which species-specific frequencies of disturbance can be predicted for a particular site. The limitations of the method and its application to questions of disturbance are also discussed.

Methods

The prediction of maximal wave-induced forces is based on the statistics of extremes as developed by Gumbel (1958). These statistics have been used to examine the probability of flooding in streams and rivers (Gumbel 1958), of extreme wind speeds (Thom 1954), jet engines "flaming out" (Jacocks and Kneile 1975), ocean wave heights (Isaacson and MacKenzie 1981), and many other phenomena (Galambos 1987). To demonstrate their utility for studying waveinduced disturbance, consider a time series of forces from which N equally long (but not necessarily contiguous) intervals, x, are chosen. The maximal force, F, in each interval is noted, and these N forces are ranked in ascending order, the smallest maximal force having rank 1 (notation defined in list of symbols). Ties are assigned a mean rank. The task is to determine the form of the probability distribution of maximal wave forces.

$$P(F) = \operatorname{Prob}[F(x) \le F]. \tag{1}$$

This probability can then be used to calculate the return time, T_{p} for each force, F:

$$T_r(F) = \frac{1}{1 - P(F)}$$
 (2)

 T_r is the number of time intervals, on average, needed to observe a wave force $\geq F$.

A simple estimate of the probability distribution of maximal forces can be obtained from the ranked sample values, F_i (where *i* is the rank of the force):

$$P(F_i) = \frac{i}{N+1} \,. \tag{3}$$

For N > 20 the relationship between F and P(F) (the cumulative probability distribution) approaches an asymptotic form,

$$P(F) = \exp - \left[(\alpha - \beta F) / (\alpha - \beta \epsilon) \right]^{1/\beta}, (4)$$

if the data are independent and identically distributed (Jacocks and Kneile 1975; discussed below). Here ϵ is the most frequently occurring F_i (mode), α measures how fast $P(F_i)$ rises with the natural logarithm of time, and the ratio α/β estimates the maximal force achievable (Jacocks and Kneile 1975).

| Significant | symbols. |
|-------------|----------|
| orgunicant | aymoons. |

| A | Characteristic area, L ² |
|------------------------|---|
| C_d, C_l | Drag and lift coefficients |
| F, \bar{F} | Maximal and mean maximal force in an |
| | interval, MLT ⁻² |
| F_n | Normalized maximal force |
| Ê | Predicted future F , MLT ⁻² |
| h | Height of individual wave, L |
| h _{rms} | Root-mean-square wave height, L |
| h_n | Normalized wave height |
| H, \bar{H} | Maximal and mean maximal wave height, |
| u | L Normalized maximal wave beight |
| 11 _n | Ronk of F |
| i r | Nalik Of F |
| J | Likelihood function |
| | Likennood function |
| N R() | No. of intervals in a sample time series |
| P(q) | Probability that a sample is $\leq q$, where |
| | q is any variable (e.g. force, height) |
| R(F) | Reduced variate of F |
| S^{2}_{F}, S^{2}_{F} | Variance of F and F, $M^2L^2\Gamma^4$ |
| Т | Wave period, T |
| $T_r(F)$ | Return time of F, intervals |
| u | Water velocity, LT ⁻¹ |
| α | Regression coefficient, MLT ⁻² |
| β | Regression coefficient |
| e | Mode of maximum force, MLT ⁻² |
| ρ | Density of water, ML ³ |
| τ | Length of interval, T |

Dimensions are in terms of mass (M), length (L), and time (T).

This distribution is often expressed as the reduced variate R(F) that transforms the distribution into a more linear form

$$R(F) = -\ln\{\ln[1/P(F)]\}.$$
 (5)

Estimating the parameters α , β , and ϵ is an exercise in nonlinear curve fitting. Several techniques have been used for extreme value statistics (Carter and Challenor 1983). We use the method of maximum likelihood estimation (Jacocks and Kneile 1975; Mendenhall et al. 1986) because its estimates have the smallest limiting variance and the limiting distribution of the estimates is normal, enabling computation of variance estimates of the parameters and confidence intervals for the predicted wave forces. The technique selects those values of the parameters that maximize the probability of obtaining the observed set of data. This probability is defined by the likelihood function (L), which is the joint probability density function, i.e. the product of the N (=total number of time intervals) individual probability density functions, dP(F)/dF, for the observed sample data. The maximum likelihood estimates of α , β , and ϵ are those that maximize the likelihood function.

$$L = \prod_{i=1}^{N} \frac{\mathrm{d}}{\mathrm{d}F} P(F_{i}, \alpha, \beta, \epsilon)$$
$$= \prod_{i=1}^{N} \exp \left[\frac{\alpha - \beta F_{i}}{\alpha - \beta \epsilon} \right]^{1/\beta}$$
$$(\alpha - \beta F_{i})^{(1/\beta - 1)} (\alpha - \beta \epsilon)^{-1/\beta}.$$
 (6)

Parameter estimates are obtained iteratively with a quasi-Newton algorithm (Wilkinson 1986).

A confidence interval for a predicted future force (\hat{F}) is derived from the variance of $(F - \hat{F})$, where F is the observed maximal force. Since the prediction and the observation are independent, the variance of the difference is estimated from the sum of the two variances, s_F^2 and $s_{\hat{F}}^2$. The latter can be calculated from the asymptotic variancecovariance matrix of the parameter estimates (Jacocks and Kneile 1975), which is commonly provided in many statistical packages with nonlinear curve-fitting modules (e.g. Wilkinson 1986).

$$s^{2}{}_{F} = \left(\frac{\mathrm{d}F}{\mathrm{d}\alpha}\right)^{2} \operatorname{var}_{\alpha} + \left(\frac{\mathrm{d}F}{\mathrm{d}\beta}\right)^{2} \operatorname{var}_{\beta} \\ + \left(\frac{\mathrm{d}F}{\mathrm{d}\epsilon}\right)^{2} \operatorname{var}_{\epsilon} \\ + 2\left(\frac{\mathrm{d}F}{\mathrm{d}\alpha}\right)\left(\frac{\mathrm{d}F}{\mathrm{d}\beta}\right) \operatorname{cov}_{\alpha\beta} \\ + 2\left(\frac{\mathrm{d}F}{\mathrm{d}\alpha}\right)\left(\frac{\mathrm{d}F}{\mathrm{d}\epsilon}\right) \operatorname{cov}_{\alpha\epsilon} \\ + 2\left(\frac{\mathrm{d}F}{\mathrm{d}\beta}\right)\left(\frac{\mathrm{d}F}{\mathrm{d}\epsilon}\right) \operatorname{cov}_{\beta\epsilon}.$$
(7)

The equation for F is derived from the inverse of Eq. 4:

$$F(R) = \alpha/\beta - (\alpha/\beta - \epsilon) \exp[-(\beta R)]$$
(8)

where R is the reduced variate (Eq. 5).

The quantity s_F^2 is given by Gumbel (1958).

$$s_F^2 = (\alpha/\beta - \epsilon)^2 [\Gamma(1 + 2\beta) - \Gamma^2(1 + \beta)]$$
(9)

where Γ is the gamma function (Abramowitz and Stegun 1964); 95% C.I. are $\hat{F} \pm t(0.975; df = n - 3)(s_{\hat{F}} + s_{\hat{F}})$. The utility of these confidence intervals for estimates outside the range of measured wave forces is obviously constrained because they are extrapolations. The predictions are only reasonable if the underlying model continues to hold.

The maximal force imposed on an organism in a given period depends on its size and shape, the topography of the shore, and the surf conditions. To compare the distribution of maximal forces among different organisms, sites, and measurement periods, we normalize the force data. Each maximal force F is divided by the mean of all maximal forces encountered during the time series, \bar{F} ,

$$F_n = F/\bar{F}.$$
 (10)

The calculations outlined above (Eq. 1-4) are then carried out with the normalized maxima, F_n . Independent probability distributions of extreme wave forces are compared by a two-sided, k-sample Smirnov test (Conover 1971).

Time series of wave-induced hydrodynamic forces imposed on limpets, barnacles, spheres, and hemispheres were obtained at intertidal sites in Washington, California, and Hawaii. In each case the experimental site was located shoreward of the break point of ambient waves (even at high tide), so that sites were subjected solely to broken waves.

The device of Denny (1983) was used to record the maximal force exerted on spheres (1,25-cm diam) during the course of each high tide over a series of tides at four rocky sites on Tatoosh Island, Washington (124°44'W, 48°24'N; Denny 1985). The interval size for these series is ~ 12 h. The directional force transducers of Denny (1982) were used to continuously monitor the force exerted on cast plastic replicas of a barnacle (Semibalanus cariosus) and a limpet [Lottia pelta, previously known as Collisella pelta (Lindberg 1986)] at an exposed rocky site on Tatoosh Island (Denny 1985; Denny et al. 1985). The maximum directional components of force occuring in each 10-min interval through the course of a high tide were noted.

A modified version of the force transducer of Denny (1982) was used to continuously measure the force exerted on a small sphere (0.8-cm diam) at two midintertidal rocky sites on the shore adjacent to Hopkins Marine Station, Pacific Grove, California (121°57'W, 36°37'N). The maximal directional components of force occurring in each 400-s interval during a period of ~ 2 h spanning high tide were measured on two occasions. In addition, the heights of the turbulent bores (broken waves) causing these hydrodynamic forces were measured with a bottom-mounted pressure transducer (Sensym 1604A) located adjacent to the force transducer. Force transducers similar to those of Denny (1982) were used to measure the drag forces exerted on small hemispheres (half a table-tennis ball) at a low rocky intertidal site on the Makapu'u Peninsula (Oahu, Hawaii, 157°39'E, 21°19'N) (Gallien 1986). The maximal shorewardseaward force occurring in each 500-s interval was noted.

The response time of the transducers used in this study is quite short [25 ms for the maximum force recorder (Denny 1983), 8 ms for the other force transducers (Denny 1982)], allowing accurate measurement of even short-duration forces. No "impact forces" were noted during these measurements (*see* Denny 1985).

Results

Although there is some variability among the eight data sets, the cumulative distributions of maximal wave forces (Fig. 1) are surprisingly similar and statistically indistinguishable (k-sample Smirnov test, P >0.1). The largest normalized force is usually ~2, and the most common normalized maximal force (i.e. ϵ) is usually ~0.8. Given the consistency of the force distributions, the data are pooled (i.e. all normalized force measurements, F_m are combined into a single data set) to provide an aggregate estimate (the solid line in Fig. 1): $\alpha = 0.414$ (SE 0.076), $\beta = 0.056$ (SE 0.076), $\epsilon = 0.810$ (SE 0.030). Thus,

$$P(F_n) = \exp\{-[(0.414 - 0.056F_n)/(0.369]^{17.9}\}.$$
 (11)

This estimate of $P(F_n)$ allows us to calculate the manner in which normalized maximal



Fig. 1. Cumulative probability distributions of normalized maximal wave forces for the eight data sets used in this study (dashed lines). The heavy solid line is the best-fit to the pooled data (Eq. 11). Samples sizes for the individual data sets ranged from 23 to 37 intervals. The two-sided, k-sample Smirnov test statistic is 0.24 (P > 0.10).

force is related to the reduced variate (Fig. 2A) or return time (Fig. 2B).

Discussion

The similarity in form of $P(F_n)$ measured over such a wide variety of sites, organisms, surf conditions, and time scales raises major questions. The first is why the probability distributions of these maximal wave forces are so similar. Because this statistical approach deals only with extreme values, a direct, mechanistic explanation for the lack of variation in $P(F_n)$ is not possible on the basis of these data alone. Different underlving distributions of water velocity and wave height could potentially have the same asymptotic distribution of extremes; therefore, different fluid-dynamic mechanisms could yield the same apparent result. It is reasonable to ask, however, whether our results are consistent with current theories regarding the nearshore flow regime, or, alternatively, whether some novel mechanism is required.

To this end we predict in turn: the distribution of maximal inshore wave heights, the maximal water velocities caused by these waves, and the maximal hydrodynamic forces caused by these velocities. In the fol-



Fig. 2. The maximum likelihood estimate of normalized maximum force as a function of (A) the reduced variate and (B) the return time. The thin lines are 95% C.L. on the best estimate.

lowing discussion we use h to designate the height of an individual wave and H to designate the maximal height in an interval of length τ .

Although the heights of breaking waves are not Rayleigh distributed, their heights after breaking closely conform to a Rayleigh distribution (Thornton and Guza 1983). Thus, the probability, P(h), that a broken wave chosen at random is less than height *h* is

$$P(h) = 1 - \exp[-(h/h_{\rm rms})^2]$$
 (12)

where $h_{\rm rms}$ is the root-mean-square wave height during the period of observation (Longuet-Higgins 1952).

To be consistent with the manner in which we earlier normalized force (Eq. 10), we divide each wave height by the mean maximal wave height, \overline{H} , of the total period of observation to give a normalized height, h_n . The probability that a wave chosen at random is $\leq h_n$ is

$$P(h_n) = 1 - \exp\{-[(h/\bar{H})^2(\bar{H}/h_{\rm rms})^2]\}\$$

= 1 - exp{-[(h_n)^2(\bar{H}/h_{\rm rms})^2]}. (13)

Longuet-Higgins (1952) has shown that in an interval of length τ , where τ is much greater than the average wave period, T,

$$(\tilde{H}/h_{\rm rms})^2 \approx \ln(\tau/T).$$
 (14)

Thus

$$\frac{P(h_n) \approx 1 - \exp\{-[(h_n)^2 \ln(\tau/T)]\}}{\approx 1 - (T/\tau)^{h_n^2}}.$$
(15)

The probability that a given h_n is of maximal normalized height, H_n , in an interval of length τ is equal to the probability that all J waves in the interval have height $< h_n$. Thus $P(H_n = h_n) = [P(h_n)]^J$. Expressing J as τ/T we see that $P(H_n)$ is

$$P(H_n) \approx [1 - (T/\tau)^{H_n^2}]^{\tau/T}.$$
 (16)

This probability can be used in Eq. 2 to calculate the return time or in Eq. 5 to calculate the reduced variate (Fig. 3). The order statistics for the extreme heights of broken waves measured at Hopkins Marine Station correspond approximately to those predicted for the Rayleigh distribution (Fig. 3).

Knowledge of the maximal wave height allows us to estimate the maximal velocity at the substratum. As a simple, first approximation we use linear wave theory, which predicts that the maximal water velocity encountered by an organism is directly proportional to wave height (Sarpkaya and Isaacson 1981).

In turn, the major hydrodynamic forces exerted on wave-swept organisms are proportional to the square of water velocity:

$$drag = \frac{1}{2\rho u^2 C_d A}$$

lift = $\frac{1}{2\rho u^2 C_f A}$ (17)

where ρ is the density of seawater, u the water velocity relative to the organism, and A a characteristic area of the organism. C_d (the drag coefficient) and C_l (the lift coefficient) depend primarily on the shape of the object, although they can have a secondary dependence on velocity. Any velocity dependence of C_d or C_l may affect the relationship between force and velocity, but the effect is typically slight for wave-swept organisms (Denny 1988).

Wave-swept organisms are also subjected to a third hydrodynamic force, the acceleration reaction. As a result, a component of the overall force is proportional to the water's acceleration rather than its velocity



Fig. 3. The reduced variate as a function of normalized maximal wave height for two sets of measurements (Λ , B) made at Hopkins Marine Station. Dotted lines are the 95% C.L. on the estimated height distribution. The observed distribution of maximal wave heights is similar to that predicted on the assumption that wave heights show Rayleigh distribution. In calculating the curve for the Rayleigh distribution we have used $\tau = 500$ s and T = 10 s-values representative of the interval lengths used and wave periods observed in our empirical measurements.

(Denny et al. 1985; Denny 1988). Because wave-swept organisms are typically small (usually $<0.001 \text{ m}^3$), however, the acceleration reaction is small relative to lift and drag (Denny 1988). As a first approximation, then, it can be assumed that the overall hydrodynamic force excrted on a waveswept organism is proportional to the square of water velocity. Therefore, given our assumption that water velocity is proportional to wave height, maximal wave forces should be proportional to the square of maximal wave heights.

If this prediction is realized in nature, the normalized maximal force predicted from linear wave theory, \hat{F}_n (= H^2/\bar{H}^2), should have the same probability distribution as the observed forces, F_n . Indeed, this pre-



Fig. 4. The probability distribution for the maximal hydrodynamic force predicted from observed wave heights and linear wave theory (circles, solid line) compared to that for observed maximal wave forces (dotted confidence intervals). A, B. The two sets of empirical observations.

diction seems valid. The order statistics for \hat{F}_n calculated from wave heights measured at Hopkins Marine Station closely resemble the regression of pooled force data (Fig. 4).

This comparison should not be construed as a rigorous test of a mechanistic model predicting maximal wave-induced hydrodynamic forces. It is possible that other models for the distribution of wave heights and water velocities could lead to the same distribution of extreme forces. Any rigorous test to discriminate among models will involve much more extensive monitoring than that carried out in the course of this study. The correspondence between the forces observed and the predictions made from simple assumptions about broken waves offers. however, an explanation for the consistency of the existing force distributions (Fig. 1) based on standard theories.

Another major issue is how this statistical approach can be used to examine disturbance. Before mechanistic predictions of

disturbance can be made, two sets of measurements must be assembled. A representative "disturbing force" (e.g. a mean breaking force and the standard deviation about this mean) must be measured for the individuals present at the site (Denny 1988). In addition, the maximal force exerted on a representative individual of the species must be measured in each of a representative series of intervals (Jones and Demetropoulos 1968; Denny 1982, 1983, 1988). Once these data are available, the statistical analysis outlined above can be used in either of two approaches to examine the probability of disturbance for a particular species at a particular site.

The first approach is a straightforward application of the statistics of extremes. The expected maximal force is predicted from the probability distribution of maximal forces— $P(F_n)$. Confidence in the predictions increases with an increase in the number of intervals, and reliable estimates often require measurements from a large number. Petrauskas and Aagaard (1971), on the basis of measurements of ocean wave heights from the Pacific coast of North America, found that uncertainty levels decreased significantly with increases in sample size up to 50. They found relative insensitivity to sample size thereafter.

The sampling effort required to predict maximal force with confidence can be decreased substantially if the similarity in form of $P(F_n)$ apparent in Fig. 1 is accepted as a universal trait of wave-swept shores. In this second approach, the probability distribution of Fig. 2B provides an estimate of the asymptotic shape of $P(F_n)$, and we need only obtain a reliable estimate of the mean maximal force at a site to convert the scale of the abscissa of Fig. 2B from normalized to absolute force. The measurement interval chosen is used to convert the ordinate from a normalized time scale (return time has the units of intervals) to one of absolute time.

With data in hand from either of these approaches, the likelihood of disturbance as a function of time can be estimated. The return time with which a particular disturbing force is exceeded can be predicted and subsequently compared, for example, with the time to first reproduction or to the average lifetime, given other sources of mortality. The predicted return times can also be compared among sites, providing a quantitative basis for comparing the relative importance of physical disturbance along environmental gradients. This measure of disturbance has the added benefit of being readily tied to demographic parameters such as survivorship. The confidence intervals about the return time estimates, together with the confidence intervals for the mean maximal disturbing force, provide a rough estimate of the range of return times expected for a given force at a particular site.

We illustrate the use of extreme order statistics by estimating the impact of wave forces on the survivorship of one species of limpet, L. pelta. The example is presented primarily as a demonstration of the methodology, rather than as an earnest prediction. For simplicity, consider a standard individual. In this case the choice of a standard is dictated by the need for an available data base. Consequently, we have chosen the individual limpet used by Denny (1985) and Denny et al. (1985) in their measurements of wave forces conducted on Tatoosh Island, Washington. The aperture area of the shell of the standard limpet is 4.19 \times 10^{-4} m². Denny (1989) measured the ability of L. pelta to resist drag (a shearing force) and lift (a tensile force). These forces are normalized to the size of the limpet by expressing them as tenacity, defined as the force required to dislodge the limpet divided by the aperture area of the shell. The mean shear tenacity is 1.67×10^5 Pa (SD = 0.60×10^5 Pa, n = 19), and the mean tensile tenacity is 1.12×10^5 Pa (SD = 0.43) $\times 10^5$ Pa, n = 16).

A mean tensile force of 46.9 newtons (N) would be required to dislodge a "standard" stationary limpet chosen at random from a population of such limpets, with a standard deviation of 18.0 N. Similarly, a mean shear force of 70.0 N would be required to dislodge a stationary limpet, with a standard deviation of 25.1 N.

These tenacity values would likely be lower if a limpet were crawling, e.g. while foraging. Miller (1974) found that the tenacity of L. pelta when moving was only



Fig. 5. Tenacity distributions for moving and stationary limpets.

36% of that when stationary. Her measurements were made with limpets adhering to an acrylic plastic substratum and the mean tenacities under these conditions are considerably lower than those measured here in the field. However, if we assume that the ratio of moving tenacity to stationary tenacity is the same for limpets adhering to rock as for those adhering to plastic and that moving limpets have the same C.V. as stationary limpets, an estimate of the tenacity of L. pelta while moving in the field can be calculated. The resulting tensile and shear forces required to dislodge the animal while it forages are: mean tensile dislodgment force (moving) = 16.9 N, SD 6.5 N; mean shear dislodgment force (moving) = 25.2 N, SD 9.1 N. From these values, we can estimate for a given force the proportion of a population dislodged or, equivalently, the probability that a random individual would be dislodged (Fig. 5). Because this calculation is based on untested assumptions (Gaussian distribution of tenacities, constant C.V. for both stationary and moving limpets), it should be treated with caution and viewed as an educated guess of the real probability of dislodgment.

Here we use as a standard sea condition the high tide of 19-20 November 1980 on Tatoosh Island. This period was used by Denny (1985) in a case study of wave forces on *L. pelta*. The surf conditions at this time were characterized by a combination of seas and swell with a period of 6-8 s. Breakers were visually estimated at 2-4 m high. Drag



Fig. 6. The probability that a limpet will be dislodged as a function of time. The dashed lines indicate the probability of dislodgment should drag or lift be decreased by 10% or, equivalently, should tenacity be increased by 10%.

forces at a rocky site shoreward of the wave's break point were recorded for ~ 6 h, and the record was divided into contiguous 10-min intervals. The maximal force was then noted for each interval and these maxima were averaged over all intervals. The mean of the maximal drag forces exerted on the standard limpet during this high tide was 1.80 N. Measurements made by Denny (1989) indicate that for L. pelta lift force is 1.75 times the drag force. Hence, the mean maximal lift force is ~ 3.15 N. These mean maximal forces are used to convert the normalized maximal force of Fig. 2B to absolute force and thereby estimate the return time for a given force acting on the limpet.

Combining these data, we estimate the probability that the standard moving limpet will encounter a force sufficient to dislodge it in a given time (Fig. 6). The limpet is much more likely to be dislodged by a lift force than by a drag force, but the probability of dislodgment for either is relatively low (a maximum of about 6% in a year). The probabilities of dislodgment for stationary limpets (which are more tenacious) would be even lower and are probably negligible. Their calculation is unwarranted because the accuracy of such estimates would rely on the distribution of tenacities to remain strictly normal even at very low probabilities—an assumption which probably stretches the analysis beyond its valid limits.

These calculations assume that the sea



Fig. 7. Probability that the offshore significant wave height $(H_{\cdot a})$ will exceed a certain value. The curve is the average of five probability distributions reported by the Coastal Data Information Program for Gray's Harbor, Ocean Park, and Long Beach, Washington (1984–1986).

conditions accounting for the mean maximal force measured on Tatoosh on 19-20 November 1980 would be present continuously. In fact, the waves present during this period are considerably higher than those typical of the Washington shore. The height of breaking waves on 19-20 November 1980 was estimated visually at 2-4 m, suggesting that the significant breaking wave height was \sim 3 m (U.S. Army Corps of Engineers 1984). If we assume that these waves have an average period of 7 s and break at a water depth equal to the wave height, simple shoaling theory predicts that the offshore (unshoaled) wave height corresponding to a 3-m breaking height is ~ 2.8 m (U.S. Army Corps of Engineers 1984).

The probability of encountering such offshore wave conditions can be estimated from information provided by the Coastal Data Information Program for various sites on the Washington coast (Fig. 7). Waves of the height observed at Tatoosh Island on 19– 20 November 1980 are present <10% of the time, and the actual probability of dislodgment will therefore be lower than calculated here. In plotting Fig. 6, we have also implicitly assumed that limpets move continuously, which is clearly false. Although this species does move to forage while the



Fig. 8. The data from Fig. 6 replotted to show the magnitude of the change in probability of dislodgment as a function of time when either lift or drag is decreased by 10%.

tide is in, as with other limpets, they are likely to stop when surf conditions are severe (Wright 1978; Judge 1988). As a consequence, these estimates of the probability of dislodgment probably are high. Because of such complications, these particular estimates should be used cautiously. They are presented primarily as a demonstration of the method by which the statistics of extremes could be used in a biological context.

This type of analysis can be applied to a variety of questions. For example, what selective advantage would a limpet accrue from a morphological change that reduced its drag or lift or increased its tenacity? If we assume either that drag and lift were reduced by 10% or that mean tenacity was increased by 10% (the standard deviation of tenacity being held constant), the probability of dislodgment is decreased (dashed lines in Fig. 6). Changes in morphology leading to a reduction in lift have a greater effect on survivorship (and are therefore substantially more susceptible to selection) than do those leading to a comparable reduction in drag (Fig. 8). Similarly, an increase in tensile tenacity has a larger effect on survivorship than does an equivalent relative increase in shear tenacity. Such differences may be especially important for morphological changes that impose tradeoffs. For example, small advantages due to decreased lift forces could easily offset large increases in drag forces.

These data can also be used to quantify

the "safety factors" associated with limpet tenacity. Here the safety factor is defined as the ratio of the force that an average limpet can resist to the maximal force that the organism will likely encounter in a specified period. If the average limpet is assumed to live between 1 and 10 yr, the safety factor for lift on a stationary limpet is about 6 while that for drag is about 10 (Fig. 9A). At shorter times, the factors of safety are considerably higher.

These factors of safety are higher than most of those estimated for other animals (Alexander 1981), where values range from 1.2 to 8, but are generally in the range of 1.5-4. Alexander noted that high values for the factor of safety are to be expected when the cost of failure is high and when the coefficient of variation in strength (here, tenacity) is high. The cost of failure in limpets is likely to be death and is therefore extremely high. The C.V. in tenacity measured by Denny (1989) is 0.36 for shear tenacity and 0.38 for tensile tenacity. These values are higher than those reported by Alexander (1981) for other animal systems, where the coefficients of variation are typically 0.1-0.3. It is probable that the high C.V. in limpets is due at least in part to an unavoidable variation in the strength of the substratum. In light of the high cost of failure and the large uncertainty in tenacity, the high safety factors calculated for stationary limpets may not be surprising.

A similar set of safety factors can be calculated for limpets that are moving and therefore have a lower tenacity. We assume as before that the tenacity while moving is 36% of that while stationary. For a lifetime of 1–10 yr, the factor of safety for drag for the average moving limpet is ~4 and the safety factor for lift is ~2 (Fig. 9B). As noted above, when the surf is rough, limpets often stop moving. As a consequence, the safety factors calculated here for moving limpets are probably lower than those expected in the field.

Caveats

There are several potential constraints on the use of these approaches. The statistics of extremes, as used here, assume that the data are independent and that the under-



Fig. 9. Safety factors for stationary (A) and moving (B) limpets.

lying distribution of forces is stationary. Both of these assumptions may be violated for wave force data. The first assumption is violated if maximal forces from contiguous sample intervals are dependent (e.g. due to multiple-day storms). The techniques outlined above, however, are reasonable as long as the dependence weakens as the time interval between samples increases (*see* Galambos 1987)—a realistic expectation for wave data. The degree of dependence in the data can also be reduced by using widely separated, rather than contiguous, intervals.

The second assumption is potentially violated by temporal trends in the maximal forces (e.g. seasonal trends in storm waves). One possible solution is to modify the cumulative probability distribution (Eq. 4) to include a time-varying component (Carter and Challenor 1981; Challenor 1982). Seasonality in wind and wave height data have been approximated by a sine function (Jardine and Latham 1981) with good results (Carter and Challenor 1981; Challenor 1982).



Fig. 10. A comparison of the probability distributions for the observed maximal forces and for the model data set taken from records of the maximum daily significant wave heights measured at the Farallon Islands, California.

Alternatively, the sampling scheme could be adjusted to diminish the effect of seasonality. For instance, Paine and Levin (1981) noted that virtually all patches in mussel beds on Tatoosh Island are created between October and April. The annual rate of disturbance would thus be estimated appropriately by measuring the maximum imposed force on days chosen randomly from the period October to April. Price (1980) has noted that the tenacity of mussels (Myt*ilus edulis*) varies seasonally, reaching a peak in winter. Thus, the above estimates of maximal force should be used in conjunction with a tenacity distribution measured during the same time of year.

If it is uncertain whether seasonal or other trends in maximal forces are present, it is necessary to sample a sufficient number of intervals to include several of any suspected periodicities. Furthermore, the interval size should be smaller than the period of the major temporal fluctuations if the time variance is to be measured and accounted for (Carter and Challenor 1981; Challenor 1982). The presence of periodicities can be ascertained with standard techniques of spectral analysis (e.g. Bendat and Piersol 1971; Chatfield 1984). Uncertainties regarding periodic trends in maximal force can thus lead to a large sampling effort in obtaining demonstrably reliable data for use in predictions. This problem may not be as serious, however, as it first appears. If day-



Fig. 11. The standard deviation of the mean maximum as a function of the number of intervals used in the estimate.

to-day, season-to-season, year-to-year, or site-to-site variations strongly affect the relationship between F_n and $P(F_n)$, the curves obtained from the various objects, sites, seasons, years, and wave conditions used in compiling Fig. 1 should not be nearly superimposable, yet they are. Further, the correspondence between imposed hydrodynamic force and the square of wave height (Fig. 4) raises the possibility that temporal trends in wave forces can be estimated from information regarding temporal trends in wave heights, for which excellent data are available.

There are two potential problems associated with using the relationship of Fig. 2 as a means of minimizing sampling effort. First, this approach relies on the universality of the relationship of F_n vs. $P(F_n)$ —an extrapolation that can only be assessed through further measurements at different sites. The correspondence between observed force distributions and that predicted from simple wave theory is, however, encouraging. Second, placing the probability distribution $P(F_n)$ on an absolute force scale relies on knowledge of the mean maximal force encountered at a site, and this value is subject to several potential measurement biases. How many intervals must one measure before a "representative" mean maximum is obtained?

Part of this problem can be addressed as follows. We use 340 sequential daily estimates of maximal significant offshore wave height at the Farallon Islands, California (Coastal Data Information Program), as a model data base. It is necessary to use a model data base rather than any of our actual measurement periods because none of the latter contain a sufficient number of intervals. This particular data base was chosen because its cumulative probability distribution is very similar to the distribution of Figs. 1 and 2 (Fig. 10). Furthermore, because this time series deals with maximal wave heights it is likely to show the same sort of temporal variation that would be encountered in a long-term measurement of wave forces on the California coast.

Measurement periods of different lengths were randomly subsampled from the overall period. Each mean of these maximal forces was normalized to the overall mean maximum of the entire period (340 intervals). The standard deviation of these normalized means was then plotted as a function of the number of sample intervals (Fig. 11). As expected, the more intervals used in estimating the mean, the greater the confidence in the estimate (i.e. the smaller the SD of means).

When each measurement period consists of contiguous blocks of intervals, the decrease in the standard deviation of means is relatively gradual. In contrast, when sample intervals are chosen at random, the decrease in variance is more rapid. This contrast is likely due to trends or periodicities in the underlying wave statistics. For example, 20 maximal wave forces measured on consecutive days in summer might yield a substantially different mean than 20 maxima measured in a similar manner in winter. Thus, seasonal or other temporal trends could lead to large variation in the estimated mean maximum among different contiguous samples.

In contrast, 20 maxima measured on randomly selected days throughout a year would provide a better estimate of the yearly mean, and thus would not be expected to vary as greatly among measurement periods. For intervals chosen at random, or contiguous intervals in a period with no underlying trend, the standard deviation is $\leq 10\%$ of the mean after only 14 intervals. It is useful that this number of samples is small. Petrauskas and Aagaard (1971) suggest that a minimal sample of nearly 50 intervals be used to reliably calculate the asymptotic relationship between H and P(H) for significant wave heights. If a similar number were required to calculate the mean maximal force, the "universal" curve of Fig. 2 would have less practical value; one would instead directly calculate the function of F vs. $T_r(F)$ for each case. Since a reliable F can apparently be calculated with substantially less sampling effort than that required to estimate the asymptotic distribution, measurements can be made at many more sites. Because these results have been obtained with a model data set and constitute extrapolation, they should be used with caution. It will be useful to repeat these calculations on an actual time series of wave-induced forces once a series of sufficient length is available.

Long-term, interannual trends in wave forces also place limits on the predictive accuracy of these techniques, particularly extrapolations to return times greatly exceeding the cumulative period of measurement. For example, significant wave heights in the northeast Atlantic have apparently increased over the past three decades (Carter and Draper 1988). As a result, predictions based on measurements within any of those years would include a potentially significant but unmeasured source of error. The extreme value approach, however, does provide a means for predicting the effects of such trends in mean maximal forces. Since the probability distribution of extreme forces appears independent of the mean maximal force, the consequences of changes in the mean are easily predicted by "sliding" the distribution along an absolute force axis. Furthermore, for many biological applications where order-of-magnitude estimates are sufficiently accurate (e.g does a breaking or dislodging force occur on average once a year, once a decade, once a century?), only large errors in estimating the mean maximal force pose any concern.

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