# Size and Survival of Intertidal Plants in Response to Wave Action: A Case Study with Fucus Gardneri

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# SIZE AND SURVIVAL OF INTERTIDAL PLANTS IN RESPONSE TO WAVE ACTION: A CASE STUDY WITH *FUCUS GARDNERI*

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*Abstract.* Hydrodynamic forces generated by breaking waves have been proposed to act as one of the primary physical mechanisms constraining the sizes to which wave-swept intertidal plants can grow. Plants inhabiting intertidal areas are generally small relative to subtidal and terrestrial plants, and within a species, plants on wave-exposed shores are usually smaller than those at wave-protected sites. However, although these relationships have been well documented, there have been no manipulative field experiments demonstrating that wave forces are directly responsible for limiting plant sizes.

In this study, I examined the effects of wave forces on plant sizes in the field by reciprocally transplanting *Fucus gardneri* (rockweed) individuals between wave-exposed and wave-protected intertidal sites at Fogarty Creek Point, Oregon. Mean sizes of wave-exposed plants transplanted to protected sites increased significantly relative to exposed control transplants. Mean sizes of wave-protected plants transplanted to exposed sites decreased significantly relative to protected control transplants.

These data support but modify an accompanying mathematical model that predicts size-dependent survivorship of *Fucus* under conditions of high and low wave exposure. This model incorporates the trade-off between higher reproductive capacity and lower probability of survival at larger plant sizes. "Optimal" plant sizes predicted by the model closely match the mean observed sizes of plants collected from exposed and protected locations. However, the match between observed and predicted plant sizes occurred not via differential survivorship, but by direct size modification resulting from plant tattering.

*Key words: disturbance;* Fucus gardneri; *intertidal macroalgae; mechanical limits; optimal size; seaweed; wave forces; wave exposure.*

## INTRODUCTION

Patterns of size in nature have long intrigued ecologists (e.g., Haldane 1928, Hutchinson and MacArthur 1960, Van Valen 1973, Peters 1983, Marquet et al. 1990). Factors influencing size distributions within populations of organisms include competition (Obeid et al. 1967, Branch 1975, Menge 1972, Wilbur and Collins 1973) and predation (Brooks and Dodson 1965, Paine 1976a, Lubchenco and Cubit 1980, Naganuma and Roughgarden 1990), as well as factors such as food availability, temperature, light, nutrient concentrations and reproductive status (Alexander 1971, Sebens 1983). However, since these factors are not mutually exclusive, it is difficult to determine the optimal size for a particular species. This optimal size is also likely to be strongly influenced by the environmental conditions typical of the habitat where that species occurs. Thus, understanding the range of environmental conditions available to a particular species and the means by which species adjust size, morphology, or life history to local conditions is critical to understanding the

distributional limits of these species and their roles in natural communities.

In shallow marine and intertidal areas, a dramatic environmental gradient exists among shores exposed to different levels of wave action. Wave action and water movement are known to influence species size, morphology, and distribution patterns, and organisms on wave-swept shores are often much smaller than those in more wave-protected habitats (Lewis 1968, Menge 1976). These trends occur both within species, and between sites of close proximity. Examples include mussels and seastars (Harger 1970, 1972, Paine 1976a,b), gastropods (Kitching et al. 1966, Behrens 1972, Etter 1989, Boulding 1990, Boulding and Van Alstyne 1993), and seaweeds (Russell 1978, Schonbeck and Norton 1981, Norton 1991).

Why then are wave-swept organisms limited to such small sizes? The implication is that conditions in the wave-exposed intertidal zone either stunt growth or break or remove organisms once they exceed a critical size. Water motion along wave-swept rocky shores produces some of the most powerful hydrodynamic forces on earth, and since such forces scale with size, they may exert selective pressures for small size. The first theoretical and quantitative effort to explore the possibility that wave forces could set mechanical limits to size in wave-swept organisms was undertaken by Den-

ny et al. (1985). Their argument was based on the concept that hydrodynamic forces acting on organisms along wave-swept shores tend to increase with increasing body size faster than the ability of the organism to maintain its attachment to the rock. Hydrodynamic forces depend on an organism's area and volume, as well as on the velocity and acceleration of the fluid past the organism. Drag is a force that increases with the square of water velocity relative to an organism and is proportional to the organism's projected area. In addition to drag, water motion in breaking waves produces a component of flow that is unsteady or accelerational; the *accelerational force* is an important additional force on organisms in an oscillatory flow. The accelerational force scales linearly with the water's acceleration and is proportional to the volume of an organism. As originally noted by Denny et al. (1985), attachment strength tends to scale with area; thus at large size, isometrically growing organisms (whose volumes increase faster than their areas) will feel increasingly large accelerational forces relative to their attachment strengths. This means that accelerational forces (acting in conjunction with drag) have the potential to set upper limits to size in wave-exposed organisms. Although Denny et al. (1985) applied this argument with some success to a variety of invertebrates, they made no attempt to explore the role of the water's acceleration in limiting the size of algae. However, Gaylord et al. (1994) recorded significant accelerational forces in a laboratory flow tank for three species of intertidal macroalgae with widely different morphologies. Gaylord et al. (1994) extended the theoretical model of Denny et al. (1985) to macroalgae, suggesting that accelerational forces may act in addition to drag to constrain the sizes at which algae survive and reproduce.

Many studies of intertidal seaweeds have documented the general trend of decreasing thallus size with increasing wave exposure in such diverse taxa as *Callithamnion* spp. (Price 1978), *Chondrus crispus* (Mathieson and Prince 1973, Dudgeon and Johnson 1992), *Corallina officinalis* (Dommasnes 1968), *Fucus* spp. (Burrows and Lodge 1951, Russell 1978) *Zonaria farlowii* (Dahl 1971), *Ulva fasciata* (Mshigeni and Kajumulo 1979), *Ulva lactuca* (Steffensen 1976), *Ascophyllum nodosum* (McEachreon and Thomas 1987), and *Sargassum cymosum* (De Paula and De Oliveira 1982). This phenomenon is not limited to marine systems. Intraspecific variations in size and morphology have also been documented in freshwater plants inhabiting streams at different flow regimes with the smallest, most turfy plants growing in the fastest flow areas (Sheath and Hambrook 1988, Brewer and Parker 1990, Chambers et al. 1991).

Despite our understanding of the relationships between plant size and wave force in the laboratory and the observed difference in thallus size across a range of water velocities in nature, the question remains whether hydrodynamic forces are the mechanism responsible for these observed patterns of size with respect to exposure. The previously described theoretical models suggesting that wave forces can set limits to size have never been experimentally tested in the field. Until recently, major impediments to extending biomechanical models to algae have been: (a) the lack of adequate models to evaluate forces on flexible objects in flow; (b) the lack of devices and models to measure and predict forces in surf zones; and (c) the lack of reliable transplant techniques to experimentally test biomechanical models in the field. Although several researchers have attempted transplants between wave-exposed and protected sites, transplants to the wave-exposed sites have generally been unsuccessful (Schonbeck and Norton 1981, De Paula and De Oliveira 1982) or only successful at lower flow, subtidal sites (Sundene 1964, Gerard and Mann 1979). Of the above impediments, (a) has been addressed by Gaylord et al. (1994) and is extended here, showing that algae experience large accelerational forces in oscillating flow that may effectively limit their maximal sizes, while (b) has been addressed by Bell and Denny (1994) and Denny (1995) and also extended here. I address (c) in this study, using reciprocal transplants of the common brown alga *Fucus gardneri* (rockweed) between wave-exposed and protected sites to investigate the hypotheses that (1) wave forces set upper limits to plant size and (2) plant survival is a function of size and wave exposure.

## METHODS

*Study location.*—This study was carried out at Fogarty Creek Point (FCP), Oregon (44°51' N, 124°03' W) 3.5 km north of Depoe Bay on the central Oregon coast. The point is a rocky (basalt) headland fully exposed to oceanic waves. Experimental plots were located on horizontal rock surfaces in the middle of the *Fucus* zone at both wave-exposed and wave-protected areas and ranged from 2.2 to 3.0 m above mean lower low water. The high-zone, wave-exposed community was dominated by *Fucus gardneri, Pelvetiopsis limitata, Mastocarpus papillatus, Endocladia muricata, Iridaea cornucopia,* and the barnacles *Balanus glandula* and *Chthamalus dalli.* The most abundant herbivores were the limpets *Lottia digitalis, L. pelta, L. strigatella,* and the snail *Littorina scutulata.* The high-zone, wave-protected community was dominated by *F. gardneri* and *M. papillatus,* with *I. cornucopia* occasionally present. The barnacles *B. glandula* and *C. dalli* were patchily present at this site and the snails *Littorina scutulata, L. sitkana,* and *Tegula funebralis* were the most abundant grazers.

*Study organism.*—*Fucus gardneri* is a common high intertidal brown alga that occurs from Alaska to Pt. Conception, California (Abbott and Hollenberg 1976). *Fucus* species are extremely plastic in their morphology (Knight and Parke 1950, Burrows and Lodge 1951, Powell 1957, Jordan and Vadas 1972). Taxonomy of
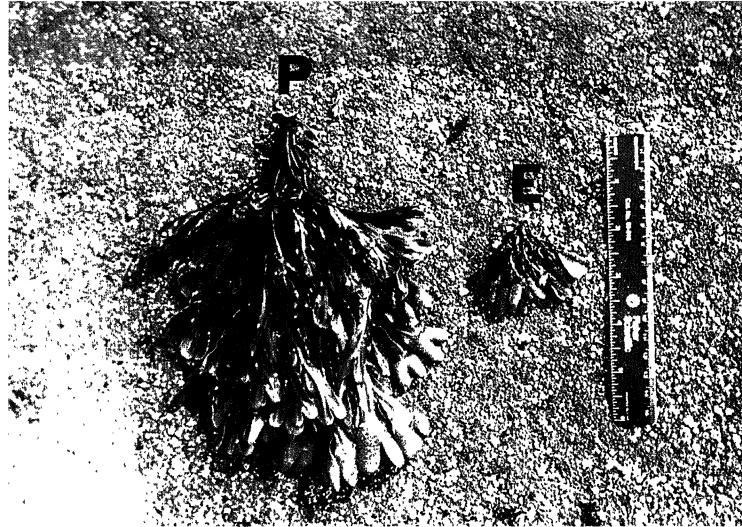
FIG. 1. Representative *Fucus gardneri* specimens collected from the wave-protected area (P) and the wave-exposed area (E).

*Fucus* species along the west coast of North America has recently been revised to include several varieties of *Fucus distichus* as *Fucus gardneri* Silva (Scagel et al. 1989). In this paper, I follow the opinion of Scagel et al. (1989) and consider the plants in this study to be *Fucus gardneri* and make no distinction among the subspecies. I refer in the rest of the text simply to *"Fucus."* Voucher specimens were collected and pressed and are held at the Hatfield Marine Science Center Herbarium (Newport, Oregon, USA).

The thallus of *Fucus* is attached by a broad discoid holdfast, from which arise bilaterally branched flattened fronds with a distinct midrib. Receptacles are present at the apices of mature plants and become swollen at the time of reproduction. Fertile plants are found in the population throughout the year, but reproduction peaks slightly in the fall and winter (Ang 1991a). Plant growth is apical and branching is dichotomous. Reproductive structures (conceptacles) develop from cells in receptacles of higher order branches. The modular character of *Fucus* means that a single plant may be reproductive throughout the year as branches reach reproductive maturity at different times. *Fucus* are perennial and can reproduce for several successive years (Ang 1991b).

*Fucus* are very abundant in the high rocky intertidal area at FCP and are highly variable in size and morphology with respect to wave exposure. "Typical" wave-exposed plants at FCP tend to be short with narrow blades and receptacles and resemble the related fucoid *Pelvetiopsis limitata,* whereas "typical" wave-protected plants have a much larger thallus with wider blades and receptacles (Fig. 1). Plants intermediate in form and size occur in intermediately wave-exposed areas between these two extremes, but in this study I focus on the extremes of this gradient. Plants used in

this study were reproductively mature and were randomly chosen from the middle of the *Fucus* zone at both sites to avoid any confounding effects of tidal height on plant size and morphology.

*Wave force measurement.*—I chose the wave-exposed and wave-protected sites within FCP after observing the intensity of wave breaking in several areas. The more seaward, wave-exposed site was located near patches of the sea palm *Postelsia palmaeformis,* which is associated with areas of extreme wave action (Dayton 1973, Paine 1979, 1988, Blanchette 1996). The more landward, wave-protected site was dominated by large *Fucus* plants. To verify and quantify my initial subjective estimates of the relative wave intensity at the two sites, I installed maximum wave force meters at both sites. Maximum wave force meters are designed to record the force imposed by the largest wave passing over the device during the time of deployment. The maximum wave force meters were developed by Bell and Denny (1994) and the spring tensions and attachment system have been slightly modified for use at FCP. Ten large eyebolts were installed at both wave-exposed and protected areas, and small carabiner quick-links were used to attach wave force meters to these bolts. Eyebolts were placed in relatively open areas at each site to avoid confounding effects of the local topography. Several wave force meters (usually between 3 and 10 meters) were deployed at each area during each sampling date. I recovered meters after 24 h and recorded measurements. Since wave force meters were not always deployed during extremely large winter storms, these measurements are an underestimate of the true maximal wave forces.

*Fucus size/strength distributions.*—To assess the seasonal and size-specific ability of plants to withstand wave action, I measured breaking forces for 100 *Fucus*

TABLE 1. Values for $x$, $y$, and $z$ are constants fit to the power curve for each date using a nonlinear, simplex, iterative procedure (SYSTAT; Wilkinson 1990). The curve describes breaking force ($F$, in newtons) as a function of plant area ($A$, $m^2$).

| Sampling date | Constants from Eq. 1 | | | $r^2$ | $P$ |
| | $x$ | $y$ | $z$ | | |
|---|---|---|---|---|---|
| March 1992 | $-16.430$ | 68.492 | 0.134 | 0.197 | $\ll 0.001$ |
| August 1992 | $-1.657$ | 96.871 | 0.276 | 0.235 | $\ll 0.001$ |
| February 1993 | $-4.279$ | 183.799 | 0.318 | 0.482 | $\ll 0.001$ |

individuals at FCP from both wave-exposed and wave-protected sites in March and August 1992 and February 1993. I placed a 10-m transect in the middle of the *Fucus* zone at each site and measured breaking forces on 10 mature (reproductive) plants haphazardly sampled from a 0.25-$m^2$ quadrat placed at each meter along the transect.

The breaking force for each plant was determined using the method of Carrington (1990). One end of a short length of string was tied to a 5000-g spring scale (Ohaus, modified to record maximum force using a rubber slider), and the other end formed a noose that was placed around the stipe (near the holdfast) of the plant. The spring scale was pulled parallel to the substratum, simulating a slowly increasing hydrodynamic force, until the thallus either detached from the rock or broke. The force required to induce this mechanical failure [maximal force ($F$)] was then recorded to the nearest 1 N.

Length of each plant ($L$) was measured from the holdfast to the tip of the longest branch and maximal projected area ($A$) was calculated by photographing each individual against a white sheet next to a ruler and analyzing plant area using an image processing program (Image 1.41, National Institute of Health). Each plant was weighed to the nearest 0.01 g after being shaken dry and blotted to remove excess water. Since the density of the algal material differs little from seawater (Gaylord et al. 1994), algal volumes were approximated by dividing masses (in kilograms) by the density of seawater (1025 kg/$m^3$).

*Probability of survival.*—Data on variation in algal strength with size were analyzed by fitting a power curve to the model remationship between plant area ($A$) and maximum force ($F$) (force at which plant was dislodged) for *Fucus* from each date (March and Au-

gust 1992; February 1993) (see Gaylord et al. 1994 for more details on the model):

$$F = x + yA^z \quad (1)$$

where $x$, $y$, and $z$ are constants fit to the power curve for each date using a nonlinear, simplex, iterative procedure (SYSTAT, Wilkinson 1990) (values for $x$, $y$, and $z$ are given in Table 1). A normalized breaking force ($f'$) was then calculated by dividing the actual measured breaking force for each plant by the breaking force predicted by the regression of this force/area relationship for each date. The cumulative probability distribution of normalized forces was then fit using a modified Weibull model (Denny and Gaines 1990, Gaines and Denny 1994):

$$\Pr(f') = \exp - \{[(a - bf')/(a - be)]^{1/b}\} \quad (2)$$

where $a$, $b$, and $e$ are constants derived from the estimation procedure (Table 2). This distribution describes the probability Pr that any given plant will break when subjected to a particular normalized force $f'$.

These normalized breaking forces were then compared to predicted hydrodynamic forces. Based on empirical data, Denny and Gaines (1990), and Denny (1991, 1993, 1995) describe the predicted maximal force ($F_{max}$) imposed on a wave-swept organism as the sum of forces due to both drag and the accelerational force:

$$\text{Drag} = (1/4)(M_{max})^2(H_m)^2 pC_d A \quad (3)$$

$$\text{Accelerational Force} = C_m pVa \quad (4)$$

$$F_{max} = \text{Drag} + \text{Accelerational Force} \quad (5)$$

where $M_{max}$ is the ratio of the predicted maximal wave height to the mean significant wave height [for the west coast of North America $M_{max} = 5.5$ for a 3-mo period (see Denny 1988, 1991, 1993, 1995, Gaylord et al. 1994 for details)] and $H_m$ is the average height of the one-third-highest waves at a particular site during a given interval of time. $C_d$ and $C_m$ are empirically measured drag and inertia coefficients of *Fucus* (0.15 and 8.00), as measured by Brian Gaylord (Hopkins Marine Station, Stanford University) using a method similar to that used by Daniel (1985), $p$ is the density of seawater (1025 kg/$m^3$), and $a$ is the acceleration imparted by the breaking wave. $V$ is plant volume, which can be expressed as an allometric function of $A$:

TABLE 2. Values for $a$, $b$, and $e$ are constants derived from the modified Weibull model fit to the cumulative probability distribution, which describes the probability Pr that any given plant will break when subjected to a particular normalized force $f'$.

| Sampling date | Constants from Eq. 2 | | | $r^2$ | $P$ |
| | $a$ | $b$ | $e$ | | |
|---|---|---|---|---|---|
| March 1992 | 0.269 | $-0.351$ | 0.636 | 0.820 | $\ll 0.001$ |
| August 1992 | 0.410 | $-0.089$ | 0.717 | 0.932 | $\ll 0.001$ |
| February 1993 | 0.554 | 0.270 | 0.829 | 0.949 | $\ll 0.001$ |

TABLE 3. Values for $f$ and $g$ are coefficients determined by a least-squares fit to the volume ($V$) and area ($A$) data using the allometric function $V = fAg$.

| Sampling date | $f$ | $g$ | $r^2$ | $P$ |
|---|---|---|---|---|
| March 1992 | 0.002 | 1.079 | 0.925 | ≪0.001 |
| August 1992 | 0.040 | 1.584 | 0.933 | ≪0.001 |
| February 1993 | 0.002 | 1.024 | 0.878 | ≪0.001 |

$$V = fA^g \qquad (6)$$

where $f$ and $g$ are coefficients determined by a least-squares fit to the volume–area data (Table 3). In this way the predicted maximal force and probability of survival for given flow conditions can be represented as a function solely of plant area.

I used the above relationships to estimate the probabilities that *Fucus* plants of different thallus areas growing along wave-exposed and wave-protected shores could survive (i.e., not be dislodged) over a 3-mo time period (i.e., a seasonal probability of survival). Thus, probability of survival in this model is equivalent to the probability that a plant will not be dislodged by waves in a given time period and is *based solely on biomechanical factors,* ignoring other biological and ecological factors (i.e., grazing, desiccation, and shading).

Few actual measurements of surf zone velocities and accelerations have been made due to both technical and practical difficulties. Based on the topography of the FCP site, swell direction, mean significant wave heights from wave buoys, maximum wave force meter recordings, and discussion with Mark Denny and Brian Gaylord (Hopkins Marine Station, Stanford University), I estimated the wave-protected site at FCP as having a mean significant wave height of 1 m ($H_m = 1$ m, a typical seasonal value for a moderately protected site) and the wave-exposed site an $H_m = 2$ m (a typical seasonal value for an exposed site) (Gaylord et al. 1994). Although there are no simple methods to estimate accelerations accompanying a given velocity in a breaking wave, I chose a reasonable range of accelerations based on previous empirical measurements (Denny et al. 1985). When organisms in the intertidal zone are hit by breaking waves, accelerations are usually large and flows are turbulent. Denny et al. (1985) recorded accelerations in the surf zone of Tatoosh Island, Washington, USA in excess of 400 m/s². Since these recordings were made during relatively calm conditions, Denny et al. (1985) estimated that accelerations as high as 1000–2000 m/s² might occur during winter storms. These accelerations are relative to rigid objects firmly attached to the rock. Algae that are flexible are likely to experience lower effective accelerations (Koehl 1984). Since wave forces at Fogarty Creek Point, Oregon, USA are likely to be similar to those at Tatoosh Island, Washington (both sites have steep offshore drop-offs and are fully exposed to oceanic

swells), I specified values of accelerations from 100 to 700 m/s² for use in Eqs. 5 and 6. These are only slightly higher than values used by Gaylord et al. (1994) for algae on the central California coast.

*Reproductive output and optimal size.*—Life history theorists have long pondered the significance of size and growth to reproduction in the evolution of life histories (e.g., Cole 1954, Stearns 1976). In an evolutionary sense, when particular traits affect both fecundity and survival, the trade-off between the two should be optimized. In a simple scenario, if we assume that reproductive output scales with size, an individual should grow as large as possible to maximize reproductive output. Ang (1992) found that mean reproductive biomass (receptacles) of a *Fucus* plant over a year comprises ≈12.7% of the total plant mass, and that this value is constant across seasons. Similarly, Vernet and Harper (1980) estimated that the eggs of various species of *Fucus* account for 0.1–0.4% of the plant's total mass. Thus an assumption that reproductive potential of a plant is proportional to volume seems appropriate. These benefits of increased reproductive capacity at large sizes may be offset by decreased survivorship. Denny et. al (1985) and Gaylord et. al. (1994) have shown that probability of dislodgment is an increasing function of size for a variety of intertidal organisms. Thus in *Fucus,* the trade-off exists between high reproductive potential and high potential for dislodgment at large sizes. Ignoring perennation and vegetative propagation due to fragmentation, Gaylord et al. (1994) calculated a value proportional to the realized reproductive output of an individual as the product of plant size (in terms of volume, $V$) and the probability that the individual of that size would survive to the time of reproduction over a specified time period ($P_s$). This yields a simple index of realized Reproductive Output (RO):

$$RO = VP_s. \qquad (7)$$

The multiplication of the $V$ and $P_s$ functions yields a curve (RO) that peaks at a size where the estimated ratio of plant benefit (in terms of reproduction) to cost (in terms of dislodgment) is highest. Thus this model allows prediction of a rough "optimal" size at which the plant potentially has a maximal realized reproductive output.

### Reciprocal transplants

To examine how plant survival is affected by size and degree of wave exposure, I reciprocally transplanted *Fucus* between wave-exposed and protected areas, monitored maximum wave forces at each site, and recorded sizes and survival of all plants over a 1-yr period. My predictions were that wave-exposed plants transplanted to wave-protected sites would not be dislodged by waves and grow large relative to exposed control plants. I further predicted that wave-protected plants transplanted to wave-exposed sites would either
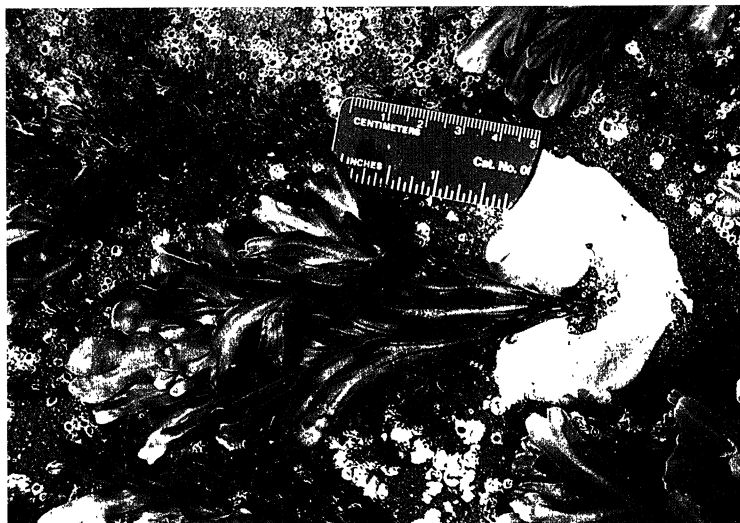
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FIG. 2. A typical wave-protected *Fucus* transplant showing the marine epoxy/rock adhesion and numbered plastic label.

be rapidly dislodged by waves or reduced in size relative to protected control plants.

*Experimental design.*—At both the wave-exposed and wave-protected sites at FCP, I randomly chose 10 mature (reproductive) plants from a 0.25-m² quadrat placed at each meter along a transect in the middle of the *Fucus* zone. I carefully chiseled out a solid section of the rock from beneath the holdfast of each chosen plant. Plants were used in the transplant experiment only if the adhesion of the holdfast to the section of rock remained firm during this process. I continued sampling until I had collected 120 plants from each site. The transplant technique involved gluing the sections of rock to which plants were attached into pre-chiseled holes at the transplant site using marine epoxy putty (Z spar, Kopper's Company, Los Angeles, California, USA) so that the transplant was flush with the surrounding rock (Fig. 2). In this way the plant's tenacity to the rock was maintained and the epoxy did not touch the plant or interfere with its growth. Each plant was individually marked by attaching a numbered plastic label to the putty.

The experimental design consisted of 60 wave-exposed plants transplanted to the wave-protected area (E to P) and 60 wave-protected plants transplanted to the wave-exposed area (P to E). Likewise, 60 wave-protected plants were transplanted back to the wave-protected area (P to P) and 60 wave-exposed plants were transplanted back to the wave-exposed area (E to E). These latter transplants served as controls for the transplant procedure. As natural controls, 60 mature, randomly chosen, naturally occurring, unmanipulated plants were followed at each site. I identified them by placing a marine epoxy spot with a numbered plastic label and arrow near the holdfast of the plant.

Since both sites (wave-exposed and wave-protected) were within 100 m of each other and at the same ef-

fective tidal height, I assume that large-scale environmental conditions such as light, temperature, and nutrient concentrations were similar between sites. Due to the greater water flows at the exposed site, nutrient exchange might actually be enhanced at this site and if anything should result in faster growth at the wave-exposed site. Densities of herbivores (primarily the snails *Littorina scutulata* and *Tegula funebralis*) were higher at the wave-protected site, and so any effects of grazing might be more intense at this site. There is no known, reliable method for determining the age of a given specimen of *Fucus*. Ang (1991*a*) followed size, growth, and mortality of a cohort of *Fucus distichus* in Vancouver, British Columbia, Canada, and found that size of *Fucus* was a better predictor of growth and mortality than age. Since I could not determine the plants' ages, I randomly chose reproductively mature individuals from each site so that size distributions were not skewed by the inclusion of juveniles.

*Data collection.*—The transplant experiment was initiated in September 1992 and lasted 1 yr. I censused the transplants and controls each month. For each individual I recorded survival (presence vs. absence), length of longest branch, planform area and approximate reproductive status. Since *Fucus* plants can perennate and regrow from a holdfast, I recorded plants as missing only when the entire holdfast was dislodged. Measuring reproductive biomass was not logistically possible without removing each plant so I subjectively assessed the relative proportion of reproductive/vegetative tissue in each plant. For each individual I determined if all (nearly 100%, scored as 4), many (≈75%, scored as 3), some (≈50%, scored as 2), few (≈25%, scored as 1), or no (scored as 0) blades on each plant bore reproductively mature receptacles.

*Data analysis.*—*Fucus* size/strength data (from the original transects at FCP) and wave force meter data
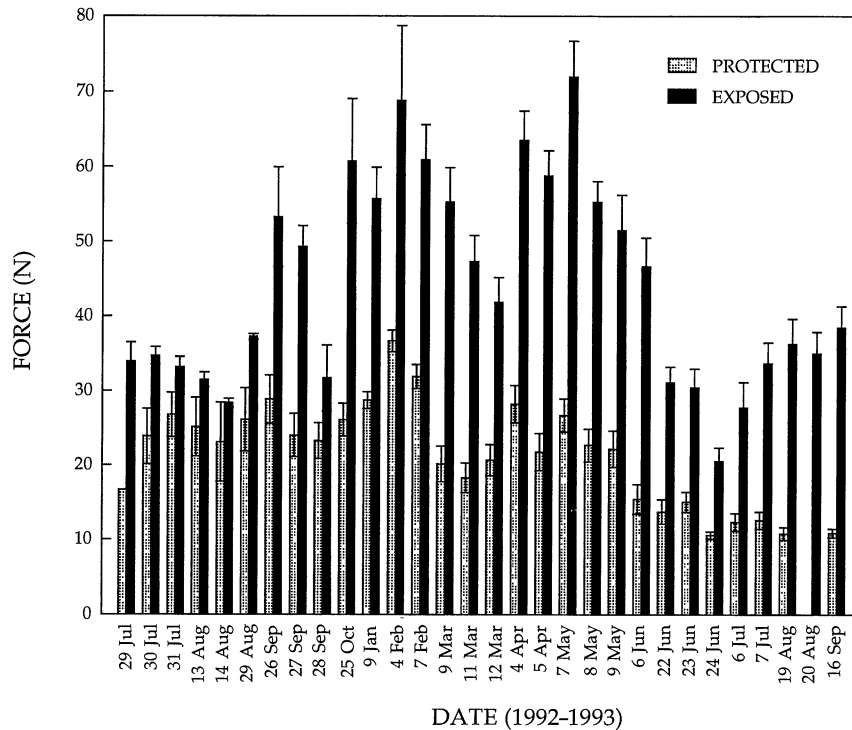
FIG. 3.  Bars represent mean maximum wave forces (N) recorded at Fogarty Creek Point, Oregon at both wave-exposed and protected sites ± 1 SEM. For most dates $n = 5$–8 wave meters.

were analyzed using a two-factor analysis of variance to determine the effects of date and wave exposure on each of the variables. To meet the assumptions of normality and variance homogeneity, data were log transformed. Survival data were analyzed using a logrank test (Hutchings et al. 1991) to compare the proportional survival of plants between the treatments and controls, and between controls and tagged plants. The size- and treatment-specific abilities of plants to survive from month to month were assessed using a two-factor analysis of variance with survival as a response variable and plant size (area), experimental treatment, and the size × treatment interaction as factors. This analysis was performed for each month of the experiment, since plant sizes changed from month to month. Repeated-measures analysis of variance (RMANOVA) on log-transformed data was employed to evaluate treatment effects on algal area and length over the 1-yr period. I compared the reproductive status of transplants and controls between wave-exposed and wave-protected sites over the 1-yr period using a two-factor ANOVA.

RESULTS

*Wave forces.*—Maximum wave force meters provided evidence that the wave-exposed area experienced forces 2–4 times greater than forces in the wave-protected area. These forces were consistently larger at wave-exposed areas than at wave-protected areas over the course of the study (one-way ANOVA effect of exposure, $P < 0.001$) (Fig. 3).

*Fucus size distributions.*—Mean sizes (areas, lengths, and masses) of *Fucus* from wave-exposed areas at all dates and at all locations were significantly smaller than those from wave-protected areas (Fig. 4) (two-factor ANOVA effects of exposure, all $P < 0.001$). Within exposures, areas and masses of plants were greater in the summer months than the winter months.

Model predictions

*Probability of survival.*—The model predicts that probability of survival should decrease as both plant size and wave exposure increase (i.e., with larger values of wave height and acceleration) (Fig. 5). The model also predicts that because of their small size, wave-exposed plants should have a very high probability of survival under wave-protected conditions (low velocities and accelerations). In contrast, the larger wave-protected plants should have very low probabilities of survival under wave-exposed conditions (high velocities and accelerations). Wave-exposed plants at wave-exposed sites are predicted to have a 30–80% probability of survival and wave-protected plants at wave-protected sites are predicted to have a 10–90% probability of survival depending on the degree of waviness (in terms of acceleration and velocity) and the time of year. Sites are likely to experience larger accelerational forces in the winter months (March and February) when weather patterns produce frequent storms than in August when wave conditions are generally more calm.
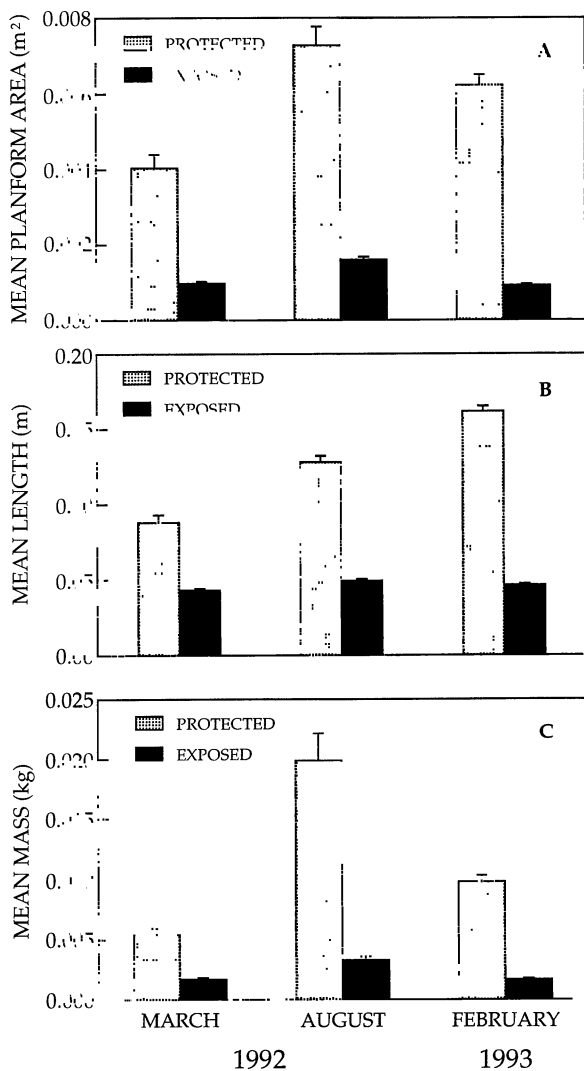
FIG. 4. Mean sizes of *Fucus gardneri* at Fogarty Creek Point, Oregon, at wave-exposed and wave-protected sites + 1 SEM in March 1992, August 1992, and February 1993. At all sites *n* = 100 plants. (a) Planform area refers to the area of the plant projected to flow, (b) length is the length from the holdfast to the tip of the longest branch, and (c) mass is the wet mass of the plant after shaking and removing surface water with a paper towel.

Accelerations of 100–200 m/s² might be typical for wave-protected sites in summer, and would probably be slightly higher in winter (200–300 m/s²). Likewise wave-exposed sites should experience lower accelerations in summer (500–600 m/s²) than in winter (600–700 m/s²). Again, since accelerations were not measured directly, these ranges are estimates based on sparse available data and should be viewed with caution.

*Index of reproductive output.*—Index of reproductive output (RO) is used only as a relative estimate, since it does not represent a precise measure of a plant's actual reproduction. However, it provides a means to examine the trade-offs between size and survival. In all cases, predicted RO (decrementing for the probability of dislodgment) increases with an increase in plant area, but only up to a certain size (Fig. 6). Above this size, low probability of survival due to hydrodynamic forces begins to offset the benefits of increased reproductive capacity at large size, and RO declines. The "optimal" size in this sense is the size at which the plant has a maximal realized reproductive output. In all cases, observed sizes of *Fucus* lie remarkably close to the optimal sizes predicted by the model, using flow conditions appropriate for the level of wave exposure and the time of year.

### Transplant experiment

*Survival.*—The number of plants remaining declined in all treatments over the course of the experiment (Fig. 7). The putty and tag were not dislodged in any cases. In all cases the percentage survival did not significantly differ over the course of the experiment between the treatments and the controls or between the controls and the tagged plants (Table 4). Contrary to the model predictions, there were no significant relationships between size, treatment, or the size × treatment interaction and survival (all $P \gg 0.05$). So, neither size nor degree of wave exposure are accurate predictors of survival for *Fucus*.

*Size.*—Mean lengths of naturally occurring tagged plants at the wave-exposed site did not differ from wave-exposed transplant controls over the entire experimental period (RMANOVA, effect of exposure, $F = 1.274$, df = 1, 66, $P = 0.271$; exposure × date, $F = 2.249$, df = 3, 66, $P = 0.091$). Similarly, mean lengths of naturally occurring wave-protected plants did not differ from wave-protected transplant controls (RMANOVA, effect of exposure $F = 0.548$, df = 1, 162 $P = 0.468$; exposure × date, $F = 0.557$, df = 10, 162, $P = 0.831$). Since naturally occurring tagged plants were not significantly different from transplant controls in terms of size or survival, I will focus on comparisons between sizes of transplants and transplant controls in the remainder of the paper. Also, patterns of mean plant lengths between treatments and over time were essentially identical to the patterns of mean plant areas. Since area better accounts for both increased extension and increased branching, I will focus on patterns of size in terms of plant areas.

Mean areas of P to P slowly increased over the course of the experiment. In contrast, mean areas of P to E sharply decreased especially during the first few months of the experiment (Fig. 8a). These P to E plants were significantly smaller than the protected control plants (RMANOVA, $F = 14.307$, df = 1, 96, $P = 0.002$) and the magnitude of this difference increased over the experimental period (RMANOVA treatment × date, $F = 11.737$, df = 8, 96, $P < 0.001$). The mean areas of E to E decreased gradually over the course of the experiment (fall and winter), however mean areas
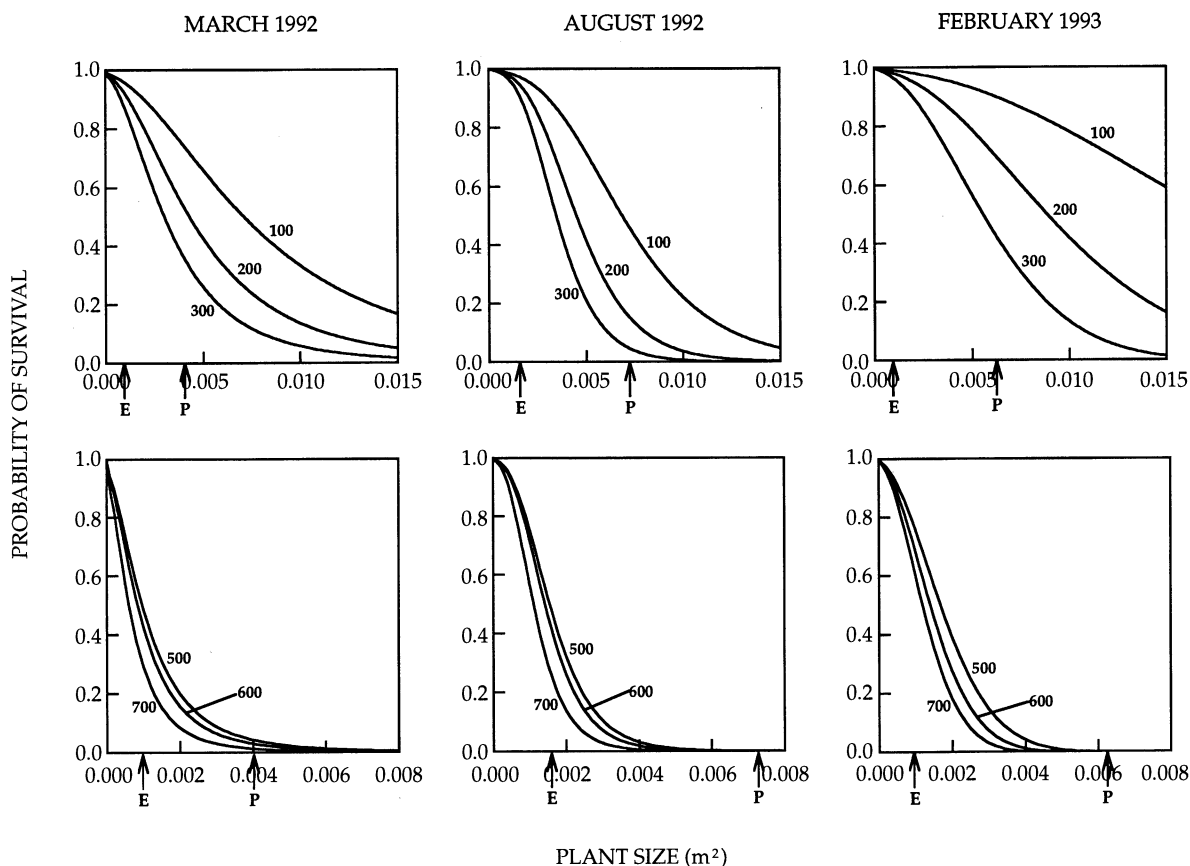
FIG. 5. The probability that a *Fucus* plant of a given size (planform area) will survive a 3-mo period at either a wave-exposed site (bottom panel) where $H_m = 2$ m or a wave-protected site (top panel) where $H_m = 1$ m, given several levels of acceleration (100–300 m/s² for the wave-protected site and 500–700 m/s² for the wave-exposed site). *Fucus* sampled in winter (February and March) are more likely to experience higher accelerations than those sampled in summer (August). The mean observed sizes of *Fucus* at each site for each date are indicated on the abcissa as E = mean observed size of wave-exposed plants, P = mean observed size of wave-protected plants. (Note different scales on the abcissa for protected vs. exposed data.)

of E to P increased over the year, particularly during spring and summer (Fig. 8b). These E to P plants grew significantly larger than the exposed control plants (RMANOVA, $F = 16.721$, df = 1, 152, $P < 0.001$) and the magnitude of this difference also increased over the experimental period (RMANOVA treatment × date, $F = 5.490$, df = 8, 152, $P < 0.001$).

If wave forces are important in limiting size, waves should prune or dislodge the largest plants. Maximum areas (area of the largest plant in each treatment) were relatively constant in both transplant controls (Fig. 8c). However, as predicted, maximum area in the P to E treatment dropped sharply in the first few months of the experiment. This was due mainly to large plants getting tattered by surf and losing branches to waves. The largest plant in this treatment was similar in size to the largest of the exposed control plants by the end of the experiment. Maximum size in the E to P treatment increased slowly over the course of the experiment due to plant growth, and maximum size of exposed plants moved to the protected site was at least

3–4 times as large as the largest wave-exposed control plant in the spring and summer. Thus although wave exposure had no effect on plant survival, plant size was rapidly and predictably affected by exposure. Wave-exposed plants avoid dislodgment by being reduced in size by loss of tissue to wave action. Once reduced in size to a range appropriate for that exposure, size alone is not an accurate predictor of subsequent survival.

*Reproductive status.*—Protected plants moved to the exposed site had fewer receptacles per thallus and a significantly lower reproductive status than protected control plants (ANOVA, $F = 59.106$, df = 1, 373, $P < 0.001$) (Fig. 9). Exposed plants moved to protected sites developed more receptacles per thallus than exposed control plants during the spring and summer (ANOVA, $F = 31.947$, df = 1, 436, $P < 0.001$). Reproductive status was also positively correlated with plant size in all treatments (i.e., the largest plants had the highest ratio of reproductive to vegetative tissue). Thus protected plants moved to the exposed site had a reduced reproductive potential, whereas exposed plants

MARCH 1992                          AUGUST 1992                        FEBRUARY 1993
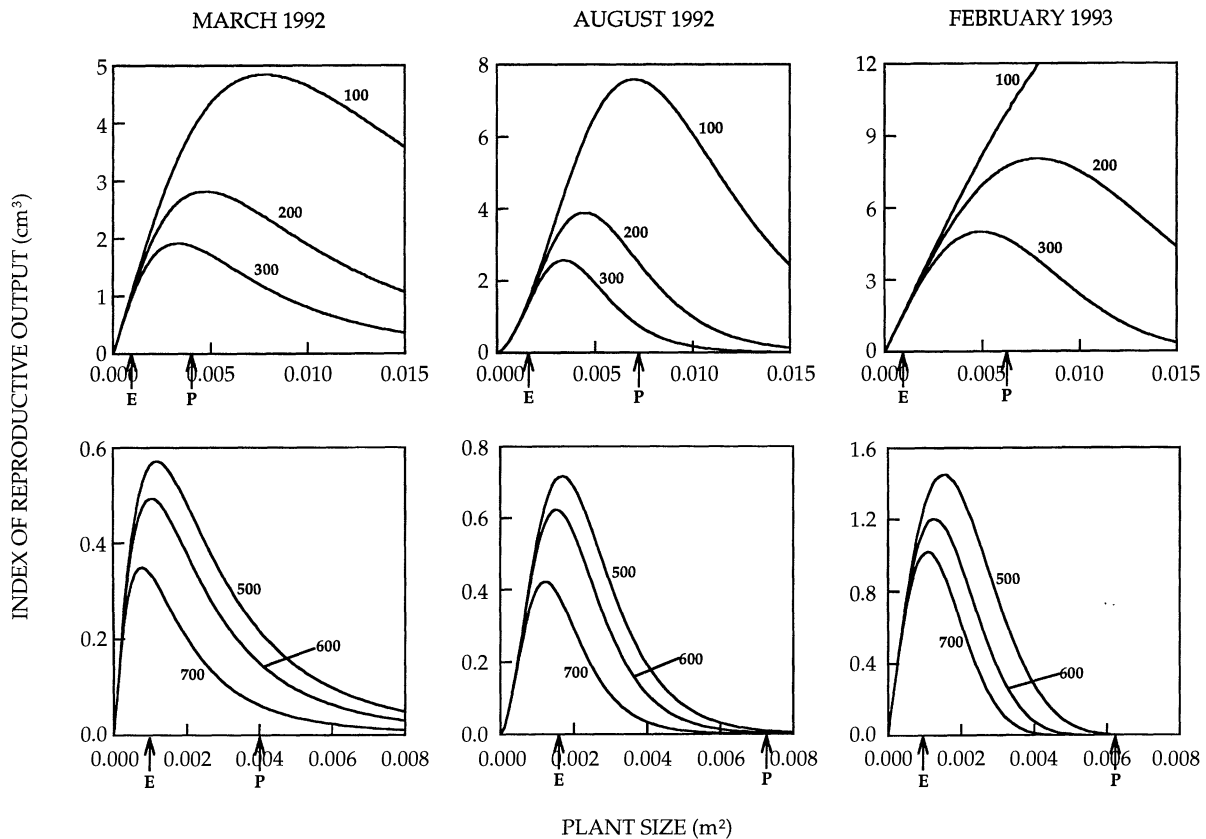


PLANT SIZE (m²)

FIG. 6.  Index of reproductive output for *Fucus* plants of various sizes (planform area) for a 3-mo period at either a wave-exposed site (bottom panel) where $H_m = 2$ m or a wave-protected site (top panel) where $H_m = 1$ m given several levels of acceleration (100–300 m/s² for the wave-protected site and 500–700 m/s² for the wave-exposed site). The mean observed sizes of *Fucus* at each site for each date are indicated on the abscissa as E = mean observed size of wave-exposed plants, P = mean observed size of wave-protected plants. Predicted optimal plant areas are near the mean sizes observed in the winter months (March and February) when accelerations are between 600 and 700 m/s² at the wave-exposed site and when accelerations are between 200 and 300 m/s² at the wave-protected site. Predicted optimal plant areas are near the mean sizes observed in August when accelerations are between 500 and 600 m/s² at the wave-exposed site and when accelerations are between 100 and 200 m/s² at the wave-protected site.

moved to the protected site grew larger and increased their reproductive capacity.

## DISCUSSION

### The relationship among size, survival, and wave exposure

Many seaweeds have been shown to exhibit a great range of morphological and size variability within a species, particularly over gradients of wave exposure (Knight and Parke 1950, Burrows and Lodge 1951, Sideman and Mathieson 1983, Armstrong 1987, Norton 1991). The sizes of *Fucus gardneri* on the Oregon coast follow this pattern of decreasing size with increasing wave exposure, and my experiments suggest that the hydrodynamic force of breaking waves is a major factor in producing this pattern.

Contrary to my original predictions and those of Denny et al. (1985) and Gaylord et al. (1994), size and wave exposure are not in and of themselves accurate predictors of survival in intertidal macroalgae such as

*Fucus*. For example, the reduction in mean size of P to E plants was not due to differential survivorship (i.e., dislodgment of large individuals) but to tattering of plants of all sizes by wave forces. These results suggest that growth form of *Fucus* in some sense allows the plant to be tailored in size by the prevailing wave climate. This generally enhances survivorship and allows the plant to grow to a near "optimal" size by keeping it at its maximum sustainable size. Since E to P plants are able to grow much larger than exposed plants, there seems to be some aspect of wave exposure that limits plant sizes. The match between observed sizes of naturally occurring *Fucus* at both extremes of wave exposure and the "optimal" sizes predicted by the model may be serendipitous, but both theory and field experiments complement each other in showing how wave action can potentially constrain size in seaweeds.

Although size in *Fucus* appears to be strongly influenced by wave action, we may not be able to make similar predictions for other intertidal algal species.
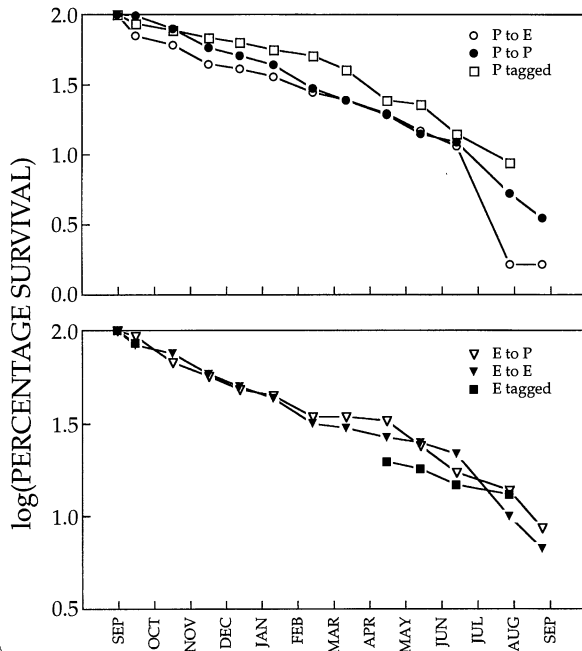
FIG. 7. Percentage of treatment and control transplants, and tagged plants surviving over the course of the experiment (shown as log scale, which results in a linear function if the probability of mortality is constant through time). Circles refer to plants from the wave-protected (P) site, triangles refer to plants from the wave-exposed (E) site, and squares represent tagged plants. Percentage survival did not differ between either the protected or the exposed treatment transplants and controls over the duration of the experiment.

The ability of *Fucus* to break and regrow may be an incidental result of its perennial, sturdy holdfast and dichotomously branched growth form. Other annual or even less sturdy intertidal species may not exist in wave-exposed locations at all, or may only seasonally occupy wave-swept sites. For example, the common, high-intertidal red alga *Mastocarpus papillatus* has a heteromorphic life history and alternates between an erect bladed form and a crustose *"Petrocelis"* phase (Zupan and West 1988). The erect-bladed forms tend to be more common during the summer, while the crustose phase persists and occupies space on the rock during the winter (E. Carrington-Bell, *personal communication* and *personal observation*). Evidence from Carrington (1990) suggests that high wave exposure in the winter is a significant agent of dislodgment for the erect blades, and that a persistent winter crust may allow *Mastocarpus* to successfully occupy space on the rock throughout the year. Algal species that have crustose or turf growth forms may not be affected by wave exposure at all, and may face greater constraints on growth from competition or herbivory. So, although *Fucus* provides a good model for an intertidal plant that occurs at all extremes of the wave exposure gradient, it is somewhat unique in its ability to occupy

TABLE 4. Comparison of proportional survival and expected mortality of plants in (a) the protected to exposed treatment (P to E) vs. the protected controls (P to P); (b) the exposed to protected treatment (E to P) vs. the exposed controls (E to E); (c) the protected to protected controls (P to P) vs. the protected tagged plants (P); and (d) the exposed to exposed controls (E to E) vs. the exposed tagged plants (E). Short-term log-rank statistics (LR) between consecutive census dates are shown, as well as $d_{1i}$ = number of deaths in group 1 at time interval $i$, $d_{2i}$ = number of deaths in group 2 at time interval $i$, $E_{1i}$ = expected number of deaths in group 1 in interval $i$, and $E_{2i}$ = expected number of deaths in group 2 in interval $i$.

| $i$ | $d_{1i}$ | $d_{2i}$ | $E_{1i}$ | $E_{2i}$ | LR | $P$ |
|---|---|---|---|---|---|---|
| a) | | | | | | |
| 1 | 18 | 1 | 9.822 | 9.178 | 14.100 | ** |
| 2 | 6 | 11 | 7.384 | 9.616 | 0.485 | NS |
| 3 | 10 | 12 | 9.927 | 12.07 | 0.001 | NS |
| 4 | 2 | 4 | 2.700 | 3.300 | 0.330 | NS |
| 5 | 3 | 4 | 3.241 | 3.759 | 0.033 | NS |
| 6 | 5 | 8 | 6.085 | 6.915 | 0.364 | NS |
| 7 | 2 | 3 | 2.500 | 2.500 | 0.200 | NS |
| 8 | 3 | 3 | 3.103 | 2.897 | 0.007 | NS |
| 9 | 3 | 3 | 3.130 | 2.870 | 0.011 | NS |
| 10 | 2 | 1 | 1.588 | 1.412 | 0.227 | NS |
| 11 | 6 | 4 | 5.000 | 5.000 | 0.400 | NS |
| 12 | 0 | 1 | 0.250 | 0.750 | 0.333 | NS |
| Year | 60 | 55 | 54.73 | 60.27 | 0.968 | NS |
| b) | | | | | | |
| 1 | 4 | 10 | 6.881 | 7.119 | 2.373 | NS |
| 2 | 15 | 5 | 10.380 | 9.615 | 4.267 | * |
| 3 | 6 | 10 | 7.429 | 8.571 | 0.513 | NS |
| 4 | 5 | 5 | 4.853 | 5.147 | 0.009 | NS |
| 5 | 2 | 4 | 2.897 | 3.103 | 0.537 | NS |
| 6 | 6 | 7 | 6.500 | 6.500 | 0.077 | NS |
| 7 | 0 | 1 | 0.513 | 0.487 | 1.053 | NS |
| 8 | 1 | 2 | 1.579 | 1.421 | 0.448 | NS |
| 9 | 5 | 1 | 3.257 | 2.743 | 2.040 | NS |
| 10 | 4 | 2 | 2.897 | 3.103 | 0.813 | NS |
| 11 | 2 | 7 | 3.913 | 5.087 | 1.655 | NS |
| 12 | 3 | 2 | 2.857 | 2.143 | 0.017 | NS |
| Year | 53 | 56 | 53.960 | 55.040 | 0.034 | NS |
| c) | | | | | | |
| 1 | 1 | 8 | 4.500 | 4.500 | 5.444 | * |
| 2 | 11 | 5 | 8.533 | 7.467 | 1.528 | NS |
| 3 | 12 | 5 | 8.596 | 8.404 | 2.728 | NS |
| 4 | 4 | 3 | 3.208 | 3.792 | 0.361 | NS |
| 5 | 4 | 4 | 3.569 | 4.431 | 0.094 | NS |
| 6 | 8 | 3 | 4.825 | 6.175 | 3.723 | NS |
| 7 | 3 | 6 | 3.326 | 5.674 | 0.051 | NS |
| 8 | 3 | 9 | 4.541 | 7.459 | 0.841 | NS |
| 9 | 3 | 1 | 1.760 | 2.240 | 1.560 | NS |
| 10 | 1 | 5 | 2.286 | 3.714 | 1.168 | NS |
| 11 | 4 | 3 | 3.267 | 3.733 | 0.309 | NS |
| Year | 54 | 52 | 48.410 | 57.590 | 1.188 | NS |
| d) | | | | | | |
| 1 | 10 | 9 | 9.421 | 9.579 | 0.070 | NS |
| 2 | 34 | 40 | 36.270 | 37.730 | 0.280 | NS |
| 3 | 1 | 1 | 1.143 | 0.857 | 0.042 | NS |
| 4 | 2 | 2 | 2.308 | 1.692 | 0.097 | NS |
| 5 | 7 | 1 | 4.727 | 3.273 | 2.671 | NS |
| Year | 54 | 53 | 53.870 | 53.130 | 0.001 | NS |

*Notes:* Expected number of deaths was calculated based on an assumption of equal probability of death for plant in any treatment. LR = log-rank statistic comparing mortality risks between the treatment and control in time interval $i$ and over the entire year:

$$LR = [(d_1 - E_1)^2/E_1 + (d_2 - E_2)^2/E_2].$$

The log-rank statistic is compared to a chi-square distribution (see Hutchings et al. 1991).
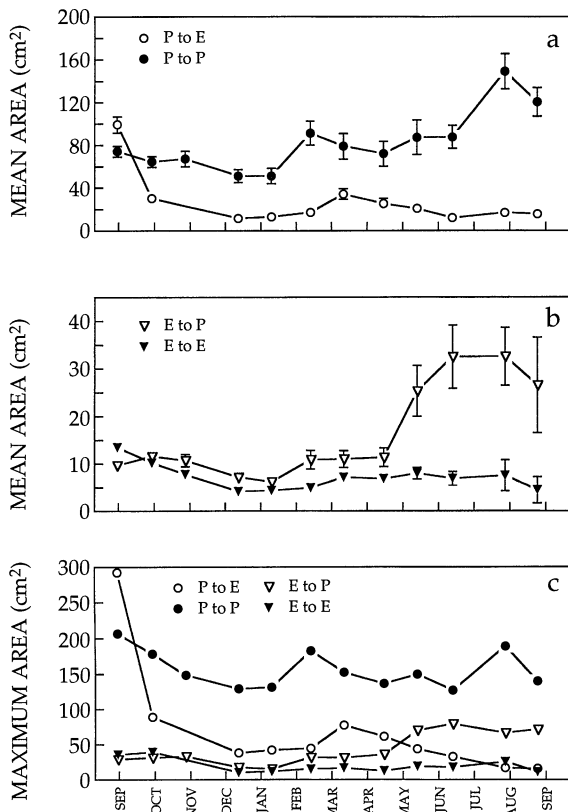
* $P < 0.05$; ** $P < 0.01$; NS = not significant.

FIG. 8. (a and b) Mean areas of plants remaining in each treatment and control group over time ± 1 SEM. Treatment transplants (E = wave-exposed transplants, P = wave-protected transplants) are represented as open symbols and controls as closed symbols. In P to E, starting $n = 60$, final $n = 1$. In P to P, starting $n = 60$, final $n = 2$. In E to P, starting $n = 60$, final $n = 5$. In E to E, starting $n = 60$, final $n = 3$. (c) Maximum area in each treatment over time.



FIG. 9. (a and b) Mean reproductive status of experimental transplants (open symbols) and controls (solid symbols) ±1 SEM. Reproductive status of each plant was scored as the number of blades on each plant containing reproductively mature receptacles: 0 = none, 1 = few, 2 = some, 3 = many, and 4 = all. E = wave-exposed transplants, P = wave-protected transplants.

this wide niche and certainly will not be representative of the responses of all intertidal plants to wave action.

### Thallus tattering

The model predicting probability of survival assumes forces above the maximal force will dislodge the entire plant from the rock and that any force below this maximal force will leave the entire plant intact. The model does not account for thallus tattering, in which individual blades or sections of the thallus are removed by waves, while the holdfast remains attached to the rock. A sublethal force may break off several branches of a plant, reducing its overall area and volume. In this case, the plant's probability of survival is increased, since the size of the plant is reduced while its tenacity remains unaffected. As evidenced in the transplant experiment, thallus tattering is common and seems to be an important method of size reduction. Thus macroalgae, such as *Fucus*, may use rapid size adjustment as a means of modifying the more traditional life history parameters of reproduction and sur-
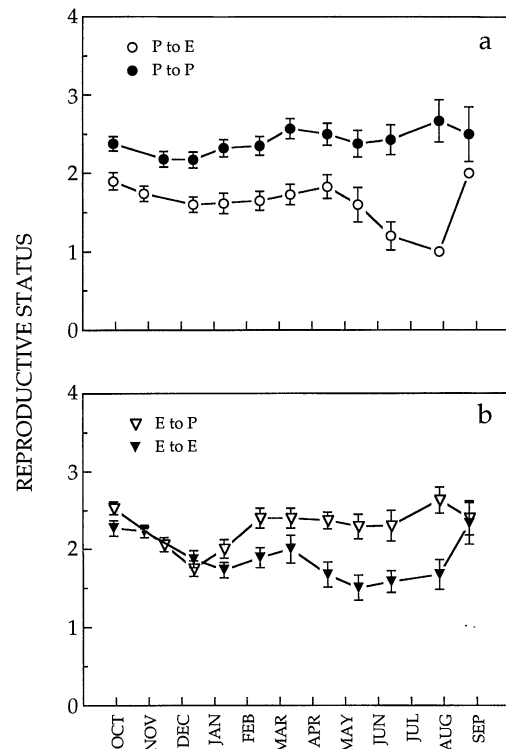
vival, to achieve some "optimal" size for a particular environment.

Besides increasing survivorship, tattering may have other benefits. Fracture may also be a useful mechanism of asexual reproduction and spore dispersal. Broken-off fragments may contain spores, conceptacles, or gametes or may be able to re-attach to the substratum and grow (Norton et al. 1982). This method of dispersal could be important in seaweeds such as *Fucus* that contain bladders or buoyant receptacles, similar to the findings of Paine (1988) that floating *Postelsia* may act as agents of long-distance dispersal. Breakage at branch points of reproductively mature receptacles could produce long-distance dispersing rafts of gametes. The simple model of this study ignores the possibility that such nonlethal pruning might account for some reproductive success in *Fucus*, and its importance remains unexplored to date.

### Seasonal effects of wave exposure

Mean and maximum wave forces at a site are directly influenced by offshore wave heights (Denny 1988). In the northeast Pacific wave heights (and therefore wave forces) are greatest in the winter months, when storms

are most frequent. This seasonal variation in wave exposure can have important implications for plant size. Plants with annual life histories can take advantage of an extended lull in wave action during summer to grow and reproduce. For example, *Nereocystis luetkeana* (the bull kelp), *Postelsia palmaeformis* (the sea palm), and *Alaria fistulosa* are annual kelps that attain very large sizes in summer, and are usually ripped from the rock by heavy wave action in winter. Alternatively, perennial plants, such as *Fucus,* have meristems that remain totipotent and are able to adjust the plant's form to adapt to prevailing conditions (Norton 1991). A plant that grows beyond the optimum size during an extended calm period, such as in summer, may be pruned back to a more sustainable size in a subsequent storm. This strategy, apparent here in *Fucus,* allows a plant to grow continually and reach a very large size/reproductive output during calm periods. As seen in the size distributions, plant sizes in summer, during periods of low waves, are considerably larger than in March or February during stormy periods (Fig. 3). Thus, under a given environmental regime, *Fucus* is able to be rapidly adjusted in size to suit local conditions as a means of modifying the more traditional life history parameters of reproduction and survival to achieve the "optimum" for that particular habitat.

### Morphological variation

Many seaweeds exhibit a great range of morphological as well as size variation across exposure gradients (Knight and Parke 1950, Burrows and Lodge 1951, Sideman and Mathieson 1983, Armstrong 1987, Gerard 1987, Norton 1991). In *Fucus,* morphology and size are both correlated with wave exposure. Wave-protected plants have wider and thicker blades than wave-exposed plants C. A. Blanchette, (*personal observation*). This pattern is common in other species of *Fucus.* Sideman and Mathieson (1985) showed that variation in morphology of *Fucus distichus* with respect to wave exposure was maintained when the progeny of the *Fucus* morphs were grown in an experimental garden. Sideman and Mathieson (1983) outplanted laboratory-cultured plants from different *Fucus* morphologies to a common garden site and found that morphology of the transplant was correlated to that of a parent plant, suggesting that the morphological variation in *Fucus* may have a genetic component. Although I have presented evidence that wave exposure can affect sizes of *Fucus,* I have no evidence for changes in morphology (i.e., blade width) and I have no evidence for or against a genetic basis to variations in morphology.

Although in some cases, plant morphology may be a potentially important determinant of the drag and accelerational forces on a plant, the evidence to date suggests that for intertidal seaweeds, size plays a more important role than shape. Carrington (1990) measured drag forces on thalli of *Mastocarpus papillatus* that varied in size and morphology. In this alga, drag force

is primarily determined by the size of the thallus and is not strongly influenced by morphology. Young (1987) studied the hydrodynamic performance of *Fucus vesiculosus* and *Ascophyllum nodosum* and also found that plant size was more critical than plant shape in determining the drag force on the thallus. The findings that within a species small size is more critical than a streamlined shape for survival on wave-swept shores tend to correlate well with some observed patterns, i.e., that plants of similar morphology tend to be progressively smaller on more exposed shores (Norton et al. 1981).

### Ecological factors affecting plant size and morphology

Ecological factors such as competition for space and grazing can influence the sizes and morphologies of plants that are present during different seasons. Schiel and Choat (1980), Cousens and Hutchings (1983), Reed (1990), and Martinez and Santelices (1992) present evidence that sizes of seaweeds may be affected by density-dependent intra- and interspecific competition. Since *Fucus* transplants in this study were all approximately uniformly spaced, it is unlikely that sizes of transplants may have been differentially affected by competition.

Levels of grazing and physical stress may also influence the size and morphology of an algal thallus within a particular life history phase. Hay (1981) has shown that algae growing in physically stressful or moderately grazed habitats tend to grow as turfs rather than spatially separated individuals. These changes in thallus morphology may be correlated with changes in size. Seasonal variations in grazing pressure have also been shown to affect plant morphology. Several annual and ephemeral high intertidal algal species have heteromorphic life histories and exist as upright morphs during the summer and as crustose or boring morphs during other seasons. The selection and continued maintenance of these different morphologies have been shown to be a function of the spatial and temporal variations in grazing (Lubchenco and Cubit 1980, Dethier 1981). The activities of grazers can also determine the points at which a plant breaks (Santelices et al. 1980). Black (1976) showed that damage by the limpet *Acmaea insessa* pruned the blades of *Egregia laevigata* (*menziesii*), making it as a whole, less susceptible to removal by waves via a reduction in size, similar to the effect of wave tattering demonstrated here in *Fucus.*

Although grazers were common at FCP, I have no evidence that sizes of transplants may have been differentially affected by grazing. The most common grazers were the limpet *Lottia digitalis* at the wave-exposed site and the snails *Tegula funebralis* and *Littorina scutulata* at the wave-protected site. Since grazers were most abundant at the protected site, effects of grazing should have been greatest there, resulting in smaller plants, which is opqosite to the observed pattern. Both

the limpet and snail grazers seem to have little effect on adult *Fucus* plants but may graze heavily on young *Fucus,* epiphytes, and other algae. Lubchenco (1983) found that *Littorina littorea* in New England harm young *Fucus,* but may actually benefit older *Fucus* by grazing epiphytes. I have observed *Littorina* and limpets grazing epiphytes on *Fucus,* but never grazing the adult *Fucus.* The limpets probably have a larger effect on the mortality of the *Fucus* by bulldozing holdfasts than on the sizes of the plants by consumption.

## Conclusions

The results of the present study provide empirical support for the idea that hydrodynamic forces can prevent plants from attaining large sizes in wave-swept intertidal areas. However, contrary to predictions from a theoretical model, size and wave exposure are not in and of themselves accurate predictors of survival in *Fucus.* Pruning by wave forces at distal branches seems to be an important method of size reduction, allowing plants to avoid dislodgment and persist during extremely wavy conditions.

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