

## INTERACTIONS BETWEEN WAVE ACTION AND GRAZING CONTROL THE DISTRIBUTION OF INTERTIDAL MACROALGAE

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**Abstract.** Canopy-forming macroalgae are key species on temperate rocky shores. However, there is a lack of understanding of how the relative balance of physical and biological factors controls the establishment and persistence of intertidal macroalgae. Here we present an integrated study of the relative importance of wave-induced forces and grazing for the recruitment and survival of the canopy-forming intertidal macroalgae *Fucus vesiculosus* and *F. spiralis*. A set of overtopped breakwaters provided a nearly unconfounded gradient in wave exposure between seaward and landward sides. A biomechanical analysis was performed based on empirical measurements of maximum drag forces in breaking waves, a model of long-term maximum wave height, and the breaking stress of *Fucus* spp. The estimated maximum flow speed (7–8 m/s) on the seaward side of the breakwaters was predicted to completely dislodge or prune *Fucus* spp. larger than ~10 cm, while dislodgment was highly unlikely on the landward side for all sizes. Experimental transplantation of *Fucus* spp. supported the biomechanical analysis but also suggested that mechanical abrasion may further limit survival in wave-exposed locations. Experimental removal of the limpet *Patella vulgata*, which was the principal grazer at this site, resulted in recruitment of *Fucus* spp. on the seaward side. We present a model of limpet grazing that indicates that limpet densities >5–20 individuals/m<sup>2</sup> provide a proximate mechanism preventing establishment of *Fucus* spp., whereas wave action >2 m/s reduces persistence through dislodgment and battering. In a conceptual model we further propose that recruitment and survival of juvenile *Fucus* spp. are controlled indirectly by wave exposure through higher limpet densities at exposed locations. This model predicts that climate change, and in particular an increased frequency of storm events in the northeast Atlantic, will restrict fucoids to more sheltered locations.

**Key words:** breaking waves; breakwaters; climate change; dislodgment; *Fucus* spp.; grazing; hydrodynamic drag; limpets; *Patella vulgata*; transplantation; *Ulva* sp.; wave exposure.

### INTRODUCTION

Canopy-forming macroalgae are a major component of communities on hard substrata in the intertidal and shallow subtidal in temperate regions worldwide. Canopy algae like *Fucus* spp., which are dominant on rocky shores throughout the northeast Atlantic, affect community structure in diverse ways, such as increasing biodiversity by creating habitats (Thompson et al. 1996) and providing refuge for predators and grazers (Black 1974, Reed and Foster 1984, Hawkins and Hartnoll 1985), and are considered as key habitat-forming species and primary producers in coastal environments (Hawkins 1981, Thompson et al. 1996). Consequently, factors controlling the distribution and abundance of canopy algae have received considerable attention. An integrated understanding of dominant factors is essential for

predictions of the distribution of intertidal macroalgae as a consequence of conservation and restoration policies (Ducrottoy 1999), and in forecasts of habitat loss caused by climate change (Thompson et al. 2002, Kendall et al. 2004).

Physical factors such as emersion stress, e.g., from insolation (Hawkins and Hartnoll 1985), and wave-induced forces (Denny 1995, Blanchette 1997), together with biotic factors including grazing (e.g., Hawkins 1981) and competition (Worm and Chapman 1998), have all been shown to influence the distribution, abundance, and fitness of canopy algae. A general pattern for fucoid macroalgae is a decline in abundance and size from sheltered to exposed locations (Lewis 1961, Stephenson and Stephenson 1972, Hawkins et al. 1992). Many environmental factors covary with exposure and may show complex interactions in their effect on fitness components of canopy-forming algae (e.g., Pratt and Johnson 2002). The only experimental tests so far of the hypothesis that exposure to wave-induced forces directly

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limits canopy algae are the studies by Blanchette (1997) and Haring et al. (2002). Blanchette (1997) used transplantation experiments to show that *Fucus gardneri* was strongly reduced in size on exposed shores with a predicted decrease in reproductive output, while Haring et al. (2002) showed that desiccation may impair mechanical properties of *F. gardneri* and lead to dislodgment, even in moderate waves. Wave exposure has also been shown to incur higher costs through extra somatic investment in holdfasts and blade thickness (Kawamata 2001).

In contrast to the scarcity of studies of wave-induced effects, there is a large body of literature showing that grazing can control the distribution of furoid algae (Jones 1946, Southward and Southward 1978, Hawkins et al. 1992). Grazing on germling and juvenile macroalgae has been suggested as a probable explanation for the decline of *Fucus* spp. on more exposed coasts, since overall grazing intensity tends to increase with exposure due to a higher density of limpet gastropods (Southward 1964, Hawkins 1983), coupled with more intensive grazing activity (Jenkins and Hartnoll 2001, Thompson et al. 2005). However, the relative importance of wave-induced forces and grazing in regulating the abundance of canopy algae on rocky shores has yet to be examined in an integrated experimental manner.

Here we examine the relative importance of wave exposure and limpet grazing in regulating the abundance of canopy-forming algae on rocky shores. Two hypotheses were tested. The first hypothesis was that elevated, wave-induced hydrodynamic forces will reduce survival and persistence of *Fucus* spp. An alternative hypothesis is that higher abundance of the limpet *Patella vulgata* on exposed shores prevents the establishment of *Fucus* spp. Both hypotheses were tested by taking advantage of a set of low-crested coastal defense breakwaters constructed of large stone boulders on the south coast of England. The breakwaters significantly reduced the wave energy on the landward side but maintained high connectivity with the seaward side, owing to the porosity of their engineering design. In this way the effect of exposure could be investigated with a minimum of confounding factors that often plague other studies, where shores with different degrees of wave exposure are separated geographically and may differ in many other aspects (e.g., Thompson et al. 2005). The effect of wave exposure was studied by transplanting *Fucus* spp. to exposed and sheltered sides of breakwaters, and by a biomechanical analysis, where estimates of maximum wave forces were compared to the adhesion strength of *Fucus* holdfasts. The effect of grazing was tested experimentally by removing limpets from plots on the landward and seaward sides of breakwaters and monitoring changes in algal recruitment and survival over time. Results from these field experiments and the biomechanical analysis were then used to formulate a quantitative model to explain how canopy-forming macroalgae are limited by both direct and indirect effects of grazing and wave exposure.

## MATERIALS AND METHODS

### Study site

This study was carried out on a series of low-crested breakwaters at Elmer near Bognor Regis on the south coast of the United Kingdom (50°47' N, 0°36' W) in 2002 and 2003. The breakwaters are parallel to the shoreline and constructed from large (1-m<sup>3</sup>) blocks of mainly granite and some limestone. These large blocks make the breakwaters highly porous, and water flowed between the seaward to the landward sides within seconds. The tide is semidiurnal with a maximum amplitude of 5.7 m. The coast is exposed, with offshore significant wave height often >3 m (4.7 m over a 5-year return period) and maximum wave periods of ~8 s. The shore has an initial slope of 1:10 and drops to ~1:70.

### General characterization of rocky-shore epibiota

The abundance and identity of macroorganisms occurring on the Elmer breakwaters were estimated from quadrat counts. A 0.25 × 0.25 m quadrat divided into a 7 × 7 grid was randomly placed on block faces 2–4 m above Lowest Astronomical Tide (LAT), and the percent cover of the biota was determined from the number of grid intersections covered by each species. The two barnacle species present (*Semibalanus balanoides* and the less common *Elminius modestus*) were not separated in these counts. For each side of the breakwaters, 32 quadrats were counted. A more detailed study was performed to determine the abundance of the dominant species *Fucus vesiculosus*, *F. spiralis*, *Ulva* (*Enteromorpha*) sp., *Patella vulgata*, and barnacles (*S. balanoides* and *E. modestus*). *F. vesiculosus* and *F. spiralis* are difficult to distinguish in the field, especially for nonreproductive individuals, and these two species also produce hybrids with intermediate phenotypes (Engel et al. 2005). We therefore classified both species and possible hybrids as *Fucus* spp. The vertical faces of 15 granite or limestone blocks (~1 m<sup>2</sup>) on both the seaward and landward sides of each of four breakwaters were examined (in total 15 × 2 × 4 = 120 blocks). The canopy of *Fucus* spp., *Ulva* sp., and barnacles were recorded as percent cover. For *P. vulgata* the number and size (in 1-cm classes) of each individual was recorded. No significant difference in distribution of epibiota on limestone and granite blocks was detected (one-factor ANOVA,  $P > 0.25$ ), so data from these rock types were pooled.

### Measurements of wave exposure

Exposure to hydrodynamic flow on the seaward and the landward sides of the breakwaters was measured both as mean flow conditions and as maximum forces of breaking waves. As a measure of the time-integrated mean flow condition, disks of gypsum (CaSO<sub>4</sub>) were bolted onto the rock surface. The dissolution of these gypsum disks provided a relative measure of water motion (e.g., Porter et al. 2000). The gypsum disks were molded in polyethylene plastic beakers using a water:

gypsum mixture of 1:1.85. A numbered tag on a metal wire was inserted into the gypsum before it solidified. The disks, ~10 cm in diameter and 2.5 cm thick, were then dried for 48 h at 60°C, allowed to cool, weighed, and stored dry until use. The gypsum disks were attached tightly to the rock surface ~3.7 m above LAT and were deployed for one or two high tides, depending on the wave intensity. Eight disks were attached on the landward and seaward side of each of two breakwaters making a total of 32 disks in each series. In addition, one set of 32 disks was deployed on the seaward side of two breakwaters at 3.0 m above LAT. This series was used to correlate dissolution rate with the angle of inclination of the rock surface. Deployments were repeated on three dates in 2002 (26 June, 1 July, and 8 July), covering a range of wave conditions. After deployment the gypsum disks were collected, dried for 48 h at 60°C, and weighed. From tide predictions for Elmer, the immersion time was estimated for each deployment, and the recorded mass loss of gypsum was converted to g/h of immersion. Mass loss of gypsum disks in a 5-L bucket kept at seawater temperature served as a still-water control and was subtracted from all measurements.

The maximum forces and flow speeds in waves breaking on the breakwaters were measured using spring-loaded gauges (Bell and Denny 1994). A hollow practice golf ball (whiffle, diameter 4 cm) was attached to a spring balance in a plastic housing bolted to the rock. Springs with maximum force extensions at 3.5 N and 15 N were used on the landward and the seaward sides, respectively. The drag force ( $F$ ) acting on the ball was converted to flow speed ( $u$ ) using the formula in (Bell and Denny 1994):

$$u = \left( \frac{F}{0.575} \right)^{0.518} \quad (1)$$

The extension of the spring was calibrated to drag force from the regression of spring extension against known weights hung from the spring. The maximum wave flow speed was measured on three different days (four replicates).

In order to predict long-term maximum hydrodynamic forces acting on *Fucus* plants, we followed the methods described in Denny (1995). The local wave climate at Elmer was estimated from a time series of significant wave height and period collected from a wave buoy (Owers Lightvessel, British Oceanographic Data Centre; 50°37' N, 0°40.8' W) 19 km west of Elmer, covering a full year (eight records per day). The temporal variation in maximum flow speed in breaking waves was modeled using linear wave theory (see Appendix). The maximum offshore wave height during a year (return time) was calculated using statistics of extremes and the joint probability of wave height and period (methods I and II in Denny [1995]).

#### *Breaking stress and drag for Fucus spp.*

Measurements of tensile strength of tissue and critical breaking stress of the holdfast were made on individual

*Fucus* spp. plants during low tides during July 2002. No *Fucus* spp. were found on the seaward side. The *Fucus* spp. examined varied from 3–48 cm in length (from holdfast to tip of longest branch). The plants were not allowed to desiccate before measurements since this may affect their material properties (Haring et al. 2002). Breaking forces were determined using the spring balance method of Carrington (1990). One end of a string was tied around the stipes of the plant, and the other end was attached to a spring balance. Two spring sizes were used with a maximum extension at about 15 N and 24 N, respectively. The spring was pulled approximately perpendicular to the mostly vertical substratum, and the force required to detach the plant from the rock or to break the tissue was recorded.

Spring gauges were also used to measure the maximum wave forces acting on plants of *Fucus* spp. Here the practice golf ball was replaced with a *Fucus* spp. plant attached with a cord around the holdfast, and the maximum extension of the spring was recorded (10 replicate plants on two days). The hydrodynamic drag acting on fronds of *Fucus* spp. was further measured in steady flow. Individual plants (length 19.5–51 cm, mass 9.1–81 g) were fixed to a spring balance and towed after a boat in the flow speed interval 1.5–6.2 m/s (speed measured by Global Positioning System). A multiple regression estimated the effect of flow speed ( $u$ , in meters per second) and plant length ( $l$ , in millimeters) on drag force ( $F$  in N) as

$$\ln(F) = 10.7 + 1.62\ln(u) + 1.85\ln(l) \quad (2)$$

( $r^2 = 0.97$ ).

No attempt was made to estimate forces due to flow acceleration (virtual buoyancy and added mass) since acceleration is expected to be insignificant on the size scale of individual *Fucus* plants (Gaylord 2000). Finally, the probability of dislodgment as a function of wave-induced drag was calculated as outlined in Denny (1995). Briefly, the size-specific variation in breaking force was estimated by fitting an allometric model to the empirical data on critical breaking stress as described (see also Fig. 3A). Measured breaking stress  $f_o$  was then normalized to the model prediction  $f_p$ :

$$f_n = \frac{f_o}{f_p} \quad (3)$$

The normalized forces were ranked in ascending order, and a cumulative probability curve was built that describes the probability that an individual will withstand a given normalized force pulling on the plant, e.g., from wave-induced drag. Using statistics of extremes the asymptotic probability distribution of the cumulative normalized forces was fitted to a three-parameter distribution of the Weibull family using a maximum likelihood criterion (e.g., Denny and Gains 2000). From this parameterization, the probability of dislodgment for any individual is easily found as a function of the drag in

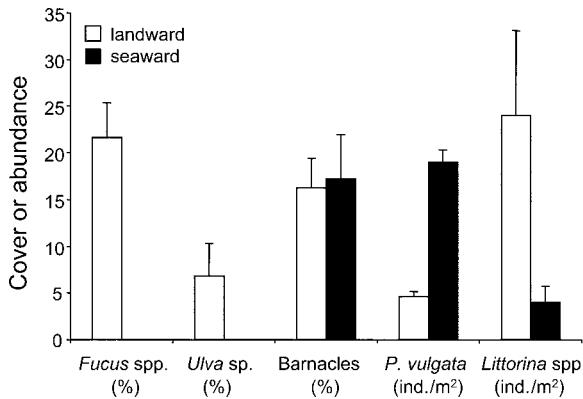


FIG. 1. Cover or abundance (mean + SE,  $n = 32$  quadrats) of dominating epibiota on the landward and the seaward sides of the Elmer breakwaters, shown as percent cover for *Fucus* spp., *Ulva* sp., and barnacles, and as number of individuals (ind.) for *Patella vulgata* and *Littorina* spp.

the tallest breaking wave predicted during an annual cycle (see Appendix).

#### Manipulation of algae and grazers

The potential for adult *Fucus* spp. to survive on the exposed seaward side was tested using a transplantation experiment. Individuals of *Patella vulgata* with *Fucus* spp. growing on their shells were removed from granite blocks on the landward side of breakwaters. Limpet shells with *Fucus* spp. offer a convenient way of transplanting algae without detaching the holdfast. The limpets were killed, and the empty shells with *Fucus* plants, ranging in size from 3–40 cm, were transplanted to the seaward side ( $n = 10$ ) and the landward side ( $n = 10$ ) of one breakwater. The limpet shells with *Fucus* plants were attached with epoxy putty ~3.7 m above LAT. The experiment continued from 4 July to 26 September 2002, and the number and length of remaining *Fucus* spp. were recorded at approximately biweekly intervals.

The possible control of *Fucus* spp. by grazing from *P. vulgata* was tested in a field experiment where the abundance of limpets was manipulated. In total, 18 granite blocks ( $\approx 1 \text{ m}^3$ ) distributed on two breakwater structures were selected for this experiment: nine on the landward and nine on the seaward side. The experimental design included three replicates of each of three treatments: total removal of limpets, partial removal of limpets (four individuals/m<sup>2</sup>), and an untouched control. Before limpets were removed, the typical abundance and size of *P. vulgata*, and the percentage cover of *Fucus* spp., *Ulva* sp., and barnacles was recorded using a 1-m<sup>2</sup> flexible quadrat. On blocks used for the total removal treatment all limpets were removed from the block surface on the breakwater. Where possible, limpets were also removed from the other faces of each block. In the partial removal treatment, all but 6 limpets/m<sup>2</sup> were removed. The blocks with the partial removal treatment were then checked after one week when the final density was adjusted to 4 limpets/m<sup>2</sup>, which was close to the average density on the

landward side. Note that this made the partial removal treatments and untouched controls essentially similar for the landward quadrats. The risk of local movement of limpets from adjacent blocks was minimal, since there were only limited areas of contact between them. Removal treatments were inspected at regular intervals (eight occasions) for 16 mo to maintain densities and record changes in the cover of algae. For the fast-growing *Ulva* sp., the average cover across all sample occasions was used to test for effects by limpet removal, while only the last recording was used for the slow-growing *Fucus* spp. The last recording of algal cover also extended the sampling area to include surfaces facing up-, down-, or sideward relative to the breakwater structure.

#### Model of limpet grazing

A simple model was formulated to evaluate the probability of a *Fucus* spp. recruit escaping grazing from the limpet *Patella vulgata*. The grazing rate of *P. vulgata* was estimated from the clearance rate of  $4.1 \times 10^{-7} \text{ m}^2/\text{s}$  (Evans and Williams 1991) multiplied by a daily activity of 5.2 h calculated from Santini et al. (2004). Recruits of *Fucus* spp. were assumed to grow at 0.07 cm/d based on Knight and Parke (1950), which is similar to the relative growth rate of 0.1–0.13/d found by Steen and Rueness (2004) for *F. spiralis* and *F. vesiculosus*. *Fucus* spp. were assumed to escape grazing mortality at a size of 3 cm (Knight and Parke 1950, Lubchenco 1983). The probability,  $P_E$ , for a *Fucus* recruit to escape grazing with rate  $g$  from  $N$  number of *P. vulgata* in a unit area is the Poisson probability:

$$P_E = e^{-gNT} \quad (4)$$

where  $T$  is the time for a recruit to grow to escape size, assuming constant linear growth. The model assumes no density-dependent effects on grazing.

#### RESULTS

##### General characteristics of epibiota on breakwaters

There was a distinct difference in the composition of epibiota between the landward and the seaward sides of the Elmer breakwaters. The major differences were the absence of macroalgae (*Fucus* and *Ulva*) on the seaward side (*Ulva* here occurred on some limpet shells), and the much lower abundance of limpets (*Patella vulgata*) on the landward side (Fig. 1). There was no clear difference in size of limpets between the landward and seaward sides of the breakwaters (two-factor ANOVA,  $F_{1,3} = 5.04$ ,  $P = 0.11$ ).

##### Flow regime on the breakwaters

Not surprisingly, the dissolution of gypsum was much higher (planned comparison contrasts,  $F_{1,85} = 36$ ,  $P < 0.0001$ ) on the seaward than on the landward side (Fig. 2A). However, the magnitude of this difference changed between dates (two-factor ANOVA,  $F_{2,85} = 123$ ,  $P < 0.0001$ ). The overall dissolution rate of gypsum covaried with offshore deepwater wave height (Fig. 2A). The

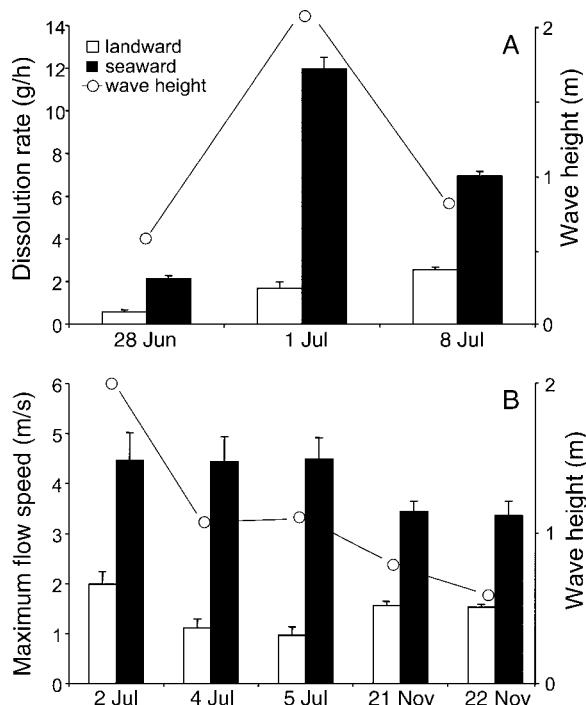


FIG. 2. (A) Dissolution rate of gypsum disks (mean  $\pm$  SE,  $n = 16$  disks) deployed on the seaward and landward sides of the Elmer breakwaters on three dates. (B) Maximum flow speed (mean  $\pm$  SE,  $n = 4$  spring-loaded gauges) in breaking waves estimated from wave gauges on the seaward and landward sides of the Elmer breakwaters. Also shown in both panels is the maximum significant wave height (open circles) at the offshore wave buoy 62305 (British Oceanographic Data Centre; see Appendix).

dissolution rate of gypsum also depended on the orientation of rock faces, being 70% higher on horizontal surfaces compared to vertical (linear regression,  $F_{1,51} = 14.1$ ,  $P = 0.0005$ ).

Fig. 2B shows the maximum flow speeds in waves breaking on the breakwater, estimated from drag-force gauges and Eq. 1. The maximum flow speed differed significantly between the landward and the seaward sides (two-factor ANOVA,  $F_{1,4} = 33.6$ ,  $P < 0.004$ ), although there was a significant interaction with the date of sampling ( $F_{4,22} = 3.1$ ,  $P = 0.036$ ). The day with the greatest difference (5 July) coincided with the neap tide with little overtopping of breakwaters during high tide, resulting in low wave action on the landward side. The speeds recorded on the seaward side between 3–5 July 2002 were underestimates, since the gauge spring was fully extended for four out of 12 recordings.

#### Model of breaking wave velocity

The time series of modeled flow velocities on the seaward side spanned a full year, and at high tide predicts maximum breaking wave heights of 3.7 m with maximum velocities around 8 m/s (see Appendix). Estimated maximum velocities were similar for methods I and II in Denny (1995). The modeled flow speeds correspond

well with the maximum speeds measured by the drag-force gauges (Appendix A). The frequency distribution of modeled flow speeds in waves breaking on the breakwaters showed that flow speed exceeds 6 m/s and 7 m/s on 18% and 7% of days, respectively. These estimates should be conservative since second-order effects such as refraction and convergence caused by bottom topography were not considered (Denny et al. 2003). Maximum flow speeds on the landward side are difficult to model and are not expected to be a simple function of breaking wave velocity. From wave gauge measurements on days with significant wave heights  $>1$  m, the maximum flow speed on the landward side was  $\sim 30\%$  of the speeds measured on the seaward side. Extrapolating over one year this suggests a maximum landward flow speed just above 2 m/s. This difference in flow speeds is also supported by the 25% lower dissolution rate of gypsum on the landward sides (Fig. 2A). The dissolution rate is expected to be approximately linear to the average flow speed (Porter et al. 2000).

#### Breaking stress of *Fucus* spp.

Most (80%) of the tested *Fucus* spp. plants showed adhesive failure between the holdfast and the rock surface. There was a significant increase in breaking stress with plant size (Spearman,  $Z = 5.7$ ,  $P < 0.0001$ ), although with considerable scatter (Fig. 3A). The measured breaking stresses were then compared to the estimated hydrodynamic drag force acting on *Fucus* spp. plants by combining modeled and recorded flow speeds in breaking waves and the measured drag forces of plants tethered to a spring balance (Eq. 2). The solid lines in Fig. 3A indicate the drag force as a function of plant size for flow speeds between 6 and 8 m/s, typical of the seaward side of the Elmer breakwaters. Based on the cumulative probability distribution of the normalized force (individual breaking force/mean breaking force) causing dislodgment, there is an annual 75% probability that a 15 cm long plant will be detached on the seaward side (Fig. 3B), while on the landward side even large individuals face only a minor risk of dislodgment ( $<5\%$ ).

*Fucus* plants that were transplanted to new sites decreased more in size (Kolmogorov-Smirnov,  $K_D = 5$ ,  $P = 0.013$ ) and in numbers (one-factor ANOVA,  $F_{1,23} = 6.74$ ,  $P = 0.016$ ) on the seaward than on the landward sides (Fig. 4). After 33 days only 20% of the plants remained on the seaward side.

#### Limpet removal experiment

In the survey on the landward side of breakwaters there was a clear negative correlation (Spearman,  $Z = -3.75$ ,  $P = 0.0002$ ) between the density of the limpet *Patella vulgata* and cover of *Fucus* spp. Experimental removal of limpets for 16 mo resulted in a significant increase in the recruitment of *Fucus* spp. on both the seaward and the landward sides of breakwaters compared to untouched control plots (two-factor ANOVA,  $F_{2,12} = 10.0$ ,  $P = 0.003$ ; Fig. 5A, B). This was particularly

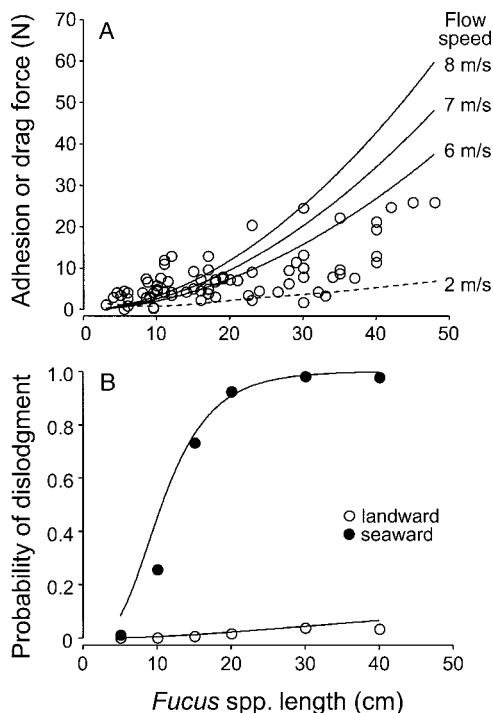


FIG. 3. (A) Critical breaking force for *Fucus* spp. as a function of plant size. The curves show the calculated drag force on *Fucus* spp. for different maximum flow speeds in waves breaking on the seaward side of the Elmer breakwaters (see Appendix). The dashed line shows estimated maximum flow speed on the landward side of the breakwaters. (B) The annual probability of dislodgment as a function of plant size for the landward and seaward sides. The curves represent fits to a three-parameter model (see Denny 1995).

dramatic on the seaward sides where no detectable recruitment occurred except on the blocks where limpet density was experimentally reduced. Higher recruitment of *Fucus* spp. was also apparent in the low-density treatment (Fig. 5A, B). Although the number of *Fucus* recruits was not statistically significant for the low limpet density (Student-Newman-Keuls test,  $P > 0.05$ ), the frequency of plots with *Fucus* spp. present was significantly higher than in control plots ( $G$  test,  $\chi^2 = 4.49$ ,  $P = 0.034$ ). Removal of limpets also led to a rapid increase in the cover of *Ulva* sp. on both the landward and the seaward sides compared to untouched control plots (two-factor ANOVA,  $F_{2,12} = 5.52$ ,  $P = 0.02$ ; Fig. 5C). In plots where limpets were removed the cover was almost four times greater on the seaward side (planned comparison contrasts,  $F_{1,12} = 7.25$ ,  $P = 0.019$ ).

When data on limpet grazing were combined into a simple model it became apparent that the area available for survival of *Fucus* spp. to a grazing-resistant size rapidly decreased to near zero at limpet densities  $>10$  individuals/m<sup>2</sup> (Fig. 6A). Even if the size that *Fucus* spp. must reach in order to escape grazing was reduced to 2 cm, a limpet density of 20 individuals/m<sup>2</sup> (as on the seaward side) resulted in  $<2\%$  of the area being ungrazed.

## DISCUSSION

Previous attempts to explain the distribution of canopy-forming algae on rocky shores have mainly examined the influence of exposure to wave action (e.g., Southward and Southward 1978, Blanchette 1997, Haring et al. 2002) or grazing by gastropods (e.g., Hawkins 1981, Jenkins and Hartnoll 2001). However, the present work is the first that experimentally separates the effects of wave-induced hydrodynamic forces from grazing in order to disentangle the relative importance of these factors, and then simulate the processes involved using simple models.

### *Distribution patterns and wave exposure*

The landward and the seaward sides of the Elmer breakwaters differed markedly in abundance of both macroalgae and grazing gastropods, mainly limpets. Notably, the seaward side completely lacked *Fucus* spp. on the entire 800-m stretch of breakwaters, while *Fucus* spp. occurred quite frequently on the landward side. The greater abundance of limpets on the seaward side and the observation that *Ulva* sp. on the seaward side only occurred on the shells of limpets strongly suggest that limpet grazing controls the abundance of algae. However, the complete absence of the canopy-forming fucoids on the seaward side could also be explained by the more severe wave climate causing dislodgment or battering of holdfasts and fronds. Empirical data and

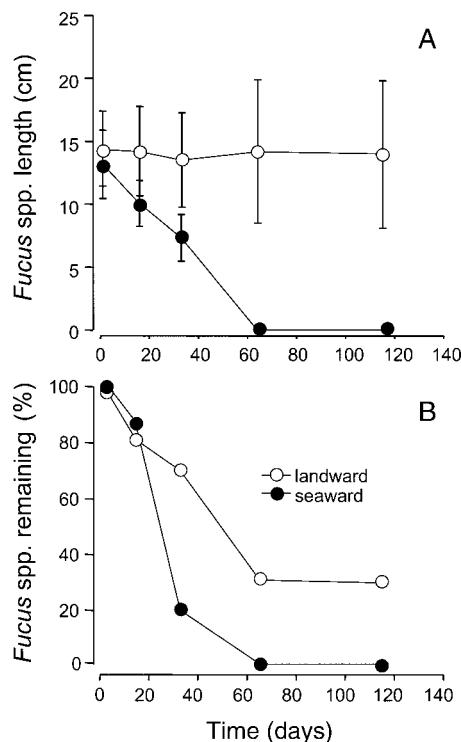


FIG. 4. The decline with time in (A) size (mean  $\pm$  SE) and (B) numbers of *Fucus* spp. transplanted to the landward and seaward sides of Elmer breakwaters.

models of wave height and maximum flow speeds revealed a big difference in flow speed between the seaward and the landward sides. The long-term maximum flow speed of 7–8 m/s estimated for the Elmer site was well within the range of maximum flow speeds for breaking waves found for other open coasts, e.g., the Canadian east coast (Hunt and Scheibling 2001) and coastal California (Gaylord 1999). Our analysis of wave-induced drag and measured breaking force showed that the estimated maximum flow speed was likely to dislodge all *Fucus* spp. of sizes larger than ~15 cm. Under certain circumstances the total force acting on the algal thallus may be larger than predicted from the drag force. Recent work by Gaylord (2000) suggests that impingement forces from waves breaking on air-exposed organisms may add at least a factor of two to the force estimated from drag caused by breaking wave velocities alone. This magnitude of impingement was compatible with measured drag differences in breaking waves (from a spring gauge) and in steady flow and would shift the maximum size of *Fucus* spp., reducing the estimated wave exposure down to 10 cm or below. The maximum breaking wave height calculated for the Elmer breakwaters assumes that the 5 m tall and steep breakwaters are almost submerged by the tide. Hence we conclude from our biomechanical model that even for this worst-case scenario, the wave-induced hydrodynamic forces on the seaward side are not sufficient to directly dislodge *Fucus* spp. <10 cm. However, the effect is likely to be of particular importance to the persistence of fucoid populations at exposed locations, since apical reproductive parts generally occur beyond this size.

Transplantation of *Fucus* spp. (Fig. 4) and a similar experiment by Blanchette (1997) suggest that fucoid algae are battered by wave exposure, and also by mechanical abrasion against the rock surface. Many of the larger individuals transplanted to the seaward side were heavily pruned, and more plants completely disappeared compared to the landward side. Since the holdfasts disappeared, dislodgment is the most probable cause of loss, although increased scour on the elevated limpet shells cannot be completely disregarded. In conclusion, it would appear that wave-induced forces may reduce the survival of *Fucus* spp. on the seaward side, at least in the size range of 5–40 cm. Haring et al. (2002) found that desiccation stress made *F. gardneri* more brittle and prone to mechanical failure even in moderate waves (flow speeds <2 m/s), mainly on sheltered sites where desiccation stress is strong. Although this mechanism may have influenced survival in our study, the absence of *Fucus* spp. on the exposed sites, and the higher survival rate of transplanted plants on the sheltered sites indicate that desiccation effects were less important.

#### Effects of limpet grazing on recruitment of *Fucus* spp.

The only locations where *Fucus* spp. recruited on the seaward sides of the eight Elmer breakwaters were where

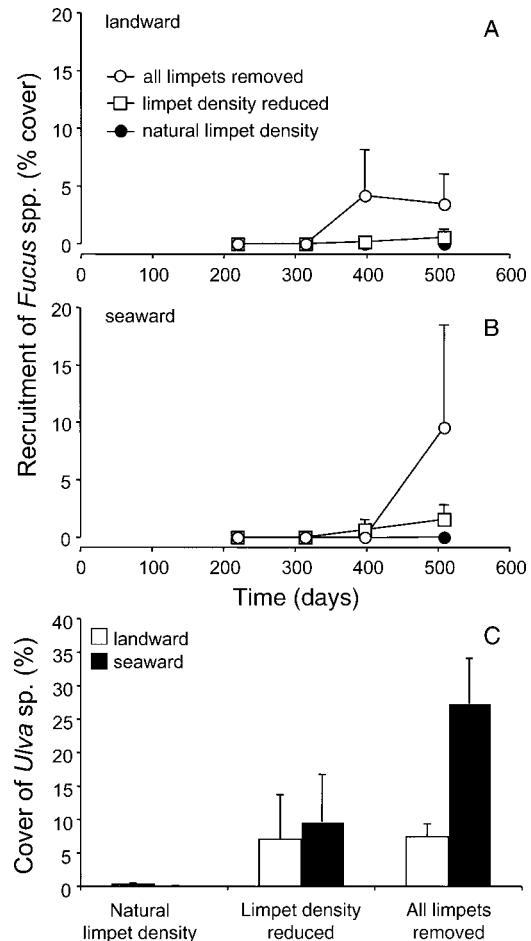


FIG. 5. Effect of experimentally reducing the density of the limpet *Patella vulgata* on algal cover; treatments included total removal of limpets, low density of limpets (~4 individuals/m<sup>2</sup>), and natural densities (~4 and 20 individuals/m<sup>2</sup> on landward and seaward sides, respectively). Effect of limpet treatments on the recruitment of *Fucus* spp., measured as percent cover (mean cover + SE,  $n = 3$  experimental plots) at (A) landward sides and (B) seaward sides of Elmer breakwaters. (C) Effect of limpet treatments on the cover of *Ulva* sp. averaged over eight sampling occasions during the 500-d experiment (mean + SE,  $n = 3$  experimental plots).

the limpet *Patella vulgata* was experimentally removed or its density reduced (partial removal). For one of the plots where limpets were removed a cover of *Fucus* spp. recruits developed over 20% of the rock surface. The lower limpet density (equivalent to the natural density on the landward side) resulted in a small but detectable increase in recruitment, indicating that this density is close to the threshold density beyond which limpets control the recruitment of *Fucus* spp. Boaventura et al. (2002) also found a dramatic increase in the recruitment of fucoid canopy-forming algae when the density of *P. vulgata* was reduced from 30 limpets/m<sup>2</sup> to near absence close to the present location (Swanage). Interestingly, most of the recruitment in the experimental plots on the seaward side occurred on rock surfaces not directly

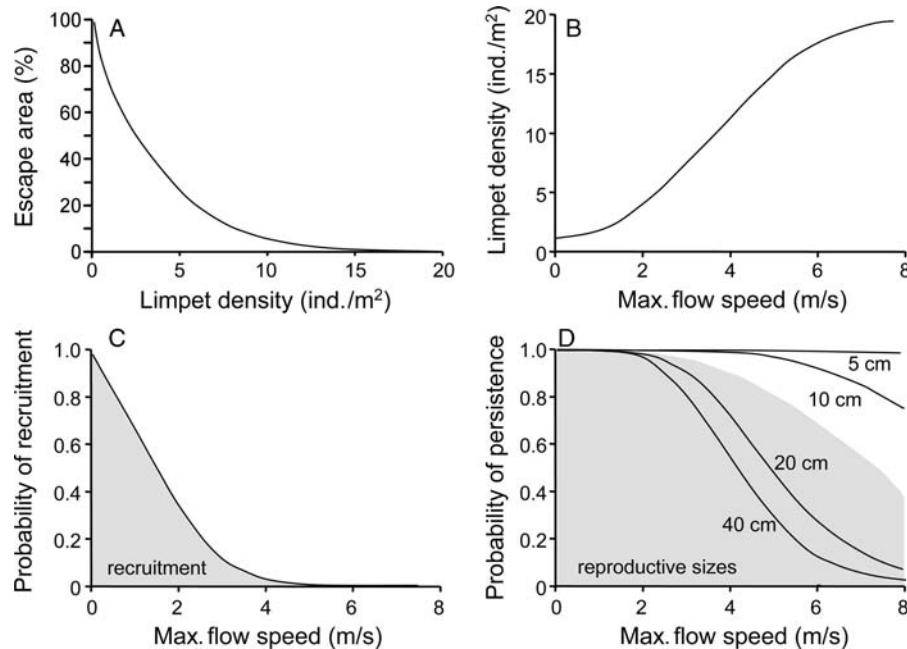


FIG. 6. (A) Model prediction of limpet grazing (Eq. 4). The curve shows the percentage of rock area where *Fucus* spp. may escape predation as a function of limpet density. (B) Schematic correlation between observed limpet density and calculated wave exposure, expressed as maximum flow in breaking waves. (C) Model of the probability of *Fucus* recruitment (shaded area) as a function of wave exposure, based on the grazing model and limpet density. (D) Persistence of *Fucus* spp. as a function of exposure and frond size, based on the empirical data on adhesion strength and modeled wave forces. The shaded area shows the sizes of *Fucus* spp. expected to have reproductive tissue.

facing the sea. This further suggests that although recruitment seems to be controlled by the presence of limpets, persistence was negatively related to wave exposure. Differences in local hydrodynamics on contrasting boulder faces were also evident from differences in dissolution rates of gypsum. The model of limpet grazing efficiency also stresses that the observed limpet density on the seaward side explains the absence of *Fucus* spp., while the lower limpet density on the landward side is expected to allow successful recruitment. These results correspond well to the conclusions reached by Southward and Southward (1978), who showed that *F. vesiculosus* could recruit on highly wave-exposed coasts following the mass mortality of limpets caused by the use of dispersants following the Torrey Canyon oil spill.

#### *Synthesis and conceptual model of factors controlling Fucus spp.*

Our study suggests that the factors controlling the distribution of canopy-forming algae like *F. vesiculosus* and *F. spiralis* interact and also differ between life stages. Based on the present field experiments and other studies of effects from wave exposure and grazing, we present a conceptual model to explain the distribution of *Fucus* spp. along a gradient of wave exposure expressed in quantitative terms as maximum flow speed in breaking waves (Fig. 6). In the absence of grazing from limpets, *Fucus* spp. will recruit even in exposed

conditions, although successful recruitment may also depend on small-scale variation in flow caused by inclination and orientation of the local substrate. Moreover, wave exposure sets an upper limit to the size of plants as a consequence of dislodgment and battering (Fig. 6D). Exposure also prunes adult plants, and since the reproductive tissue is located at the apical ends, this reduces reproductive output. If limpets exceed some critical density (in this study 5–20 limpets/m<sup>2</sup>), recruitment of *Fucus* spp. is prevented through grazing (Fig. 6B, C). In sheltered conditions wave exposure is not sufficient to damage even large plants of *Fucus* spp., and the lower density of limpets (<5 limpets/m<sup>2</sup>) allows for the recruitment of *Fucus* spp. Thus the proximal driving factor of the observed distribution of *Fucus* spp. on the breakwaters at Elmer is the difference in limpet densities between the landward and the seaward sides. What causes this difference in limpet density? *Patella vulgata* generally occurs at higher densities on exposed shores (e.g., Lewis 1964, Hawkins et al. 1992), and it has been suggested that the density of limpets may be controlled by suitable habitats for recruitment (e.g., Bowman 1981), by interference with established macroalgae (e.g., Jenkins et al. 1999), or by the production of the biofilm-based food resource (e.g., Thompson et al. 2004, 2005). Although limpets can feed on fucoids on sheltered shores, these shores usually have low recruitment of limpets due to space occupation by turf-forming algae.

However, at the tidal heights studied, turfs were absent on the Elmer breakwaters, so this cannot explain the patterns observed. Recruitment of *P. vulgata* is also known to require pools or damp microenvironments (Bowman 1981) that will occur more frequently at exposed sites. The more rapid recruitment or growth rate of *Ulva* sp. on the seaward side of the Elmer breakwaters (Fig. 5C) suggests that, for ephemeral macroalgae at least, production was higher on the wave-exposed side.

In conclusion, it would appear that grazing limits establishment of *Fucus* spp., while wave action affects persistence of individuals once established. Our model contrasts to the interaction between grazing and hydrodynamic flow found by Duggins et al. (2001) for a subtidal kelp in the northeast Pacific. They found that grazers could regulate the abundance of kelp only at intermediate current speeds. A conceptual model explained this in terms of the relative strength of kelp stipes and the flow-induced drag force where tissue strength was a negative function of gastropod grazing. Where tidal currents were slow, the drag force could not break kelp plants despite tissue damages caused by intense gastropod grazing, while strong tidal currents reduced grazer presence and tissue strength remained above the drag force acting on the kelp. There are two major differences between the subtidal environment in Duggins et al. (2001) and the rocky shores in our study that explain the contrasting model predictions: the flow speeds in breaking waves are substantially higher than subtidal orbital flow or tidal currents, and limpets can tolerate even the extreme drag forces in 10-m tall breaking waves (Denny 1988). Thus the impressive tenacity of limpets results in strong biological control. However, the increasing limpet abundance with wave exposure shows how physical forcing modifies the strength of this plant–herbivore interaction, with implications for distribution patterns.

Changes in physical forcing due to global warming may shift plant–herbivore interactions, altering community structure and ecosystem functioning both in terrestrial (Post and Stenseth 1999) and marine ecosystems (Schiel et al. 2004). Our model predicts that climate change may modify the interactions between limpets and fucoids through changes in the physical environment. Climate change forecasts for the northeast Atlantic suggest that there will be hotter summers and wetter, windier, and hence stormier winters (Hulme et al. 2002). Both will influence the likelihood of furoid establishment: desiccation will inhibit early growth of germlings (Thompson et al. 2004), and temperature rise may favor limpets (Schiel et al. 2004), reducing the probability of escaping grazing; stormier seas will dislodge adult plants and favor limpets. Therefore in a warmer world we predict fucoids to become increasingly restricted to more sheltered locations over much of their range in northern France, Britain, and Ireland, as is now found further south in Europe (Ladah et al. 2003).

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#### APPENDIX

A model of wave breaking and maximum flow speed (*Ecological Archives* E087-067-A1).