

Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality*

Robert L. Vadas, Wesley A. Wright, Steven L. Miller**

Department of Botany & Plant Pathology, University of Maine, Orono, Maine 04469, USA

ABSTRACT: The brown alga *Ascophyllum nodosum* (L.) Le Jolis is a dominant rocky intertidal organism throughout much of the North Atlantic Ocean, yet its inability to colonize exposed or denuded shores is well recognized. Our experimental data show that wave action is a major source of mortality to recently settled zygotes. Artificially recruited zygotes consistently exhibited a Type IV survivorship curve in the presence of moving water. As few as 10, but often only 1 relatively low energy wave removed 85 to 99% of recently settled zygotes. Increasing the setting time for attachment of zygotes (prior to disturbance from water movement) had a positive effect on survival. However, survival was significantly lower at high densities, and decreased at long (24 h) setting times, probably as a result of bacteria on the surface of zygotes. Spatial refuges provided significant protection from gentle water movement but relatively little protection from waves. These data indicate that zygotes are maladapted for attachment in moving water and suggest that water movement is the primary factor controlling recruitment and distributional patterns of *A. nodosum*. These and earlier observations on the long-term lack of colonization of denuded shores suggest that successful recruitment is highly episodic on all but the most sheltered shores. Because of the widespread dominance of *A. nodosum*, disturbance by waves or currents, and stochastic events may play major roles in structuring intertidal communities in the Northwest Atlantic.

INTRODUCTION

Wave action is generally considered an important factor in the distribution and abundance of intertidal organisms. There are, however, few quantitative data on the specific effects of waves on patterns of species abundance. Biological exposure scales describe the direct or indirect effects of waves (Ballantine 1961, Dalby et al. 1978), but they do not characterize what aspects of wave energy are important to the dynamics of a species. Attempts to quantify wave forces are noteworthy (Jones & Demetropoulos 1968, Harger 1970, Doty 1971), although they all have limitations (Denny 1985a). In general, little attention has been paid to measuring abiotic forces on rocky shores (Palumbi 1984).

Waves affect intertidal communities by damaging individuals and by displacing plants and animals, either individually or in groups (Schwenke 1971, Con-

nell 1972, Grant 1977, Vadas 1979, Denny et al. 1985). Wave energy also causes indirect mortality to juvenile and adult assemblages through movement of algal fronds, logs, rocks and debris (Connell 1961, Dayton 1971, Velimirov 1983, Sousa 1984). Considerably less is known about the effects of wave forces on juvenile stages of marine organisms. Wave action, however, directly reduces the density of newly recruited barnacles (Ortega 1981). Few studies have analyzed wave effects on recruiting or juvenile algae. Nonetheless, such data may be essential for understanding the abundance patterns and dynamics of a species and community organization (Sebens & Lewis 1985).

Along the northern Gulf of Maine the dominant intertidal organism is the brown alga *Ascophyllum nodosum* (L.) Le Jolis (Keser et al. 1981, Topinka et al. 1981, Vadas & Wright 1986). Despite its abundance on these and other North Atlantic shores, 2 striking patterns are apparent: a marked decline or absence of plants (especially juveniles) on wave-exposed shores and a general lack of recruitment on all shores (Oltmanns 1889, deVirville 1953, Printz 1956, Boney 1966, Baardseth 1970). Twenty years of observation at Lamoine Maine, USA, revealed no successful coloniza-

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** Present address: NURC-FDU, #40 Estate Castle Coakley, St. Croix, U.S. Virgin Islands 00820

tion by *A. nodosum* despite its abundance at this and adjacent sites (Vadas & Wright 1986). This particular population has noticeably declined in cover during the last 5 to 10 yr. Several other sites in Maine show similar recruitment patterns, with few exceptions (Keser & Larson 1984).

Although *Littorina littorea* (L) grazes on or disturbs sporelings of *Ascophyllum nodosum* (Sundene 1973, Watson & Norton 1985, Patterson 1986), cage experiments designed to exclude this herbivore have produced only one natural recruit since 1972 (Vadas unpubl.). Moreover, attempts to recruit *A. nodosum* artificially by pouring zygotes over numerous caged natural surfaces have also failed to produce significant recruitment (Vadas & Wright 1986). This apparent enigma, the dominance of *A. nodosum* and the concurrent lack of visible recruitment on these and European shores, raises the question of what controls colonization?

Here we examine recruitment and early survival (≤ 24 h) of zygotes in artificial and natural wave energy environments as a function of setting or attachment time, density and surface texture. In particular, we address the following questions: (1) Does wave action affect recruitment and, if so, what controls its effect? (2) Does setting or attachment time affect recruitment? (3) Are refuges important to recruitment and early survival? Our experiments demonstrate that wave action, and water motion in general, is a major source of mortality to zygotes of *Ascophyllum nodosum*. Longer setting times and refuges enhance survival but only in gentle flowing waters. These results suggest that zygotes of *A. nodosum* are maladapted to water movement, and that natural recruitment is episodic, except perhaps on very sheltered shores and among holdfasts in dense stands.

METHODS

Pottery chips were used as a synthetic substrate for recruitment because of their favorable attachment qualities, water holding potential and ease of removal for sampling (Hanic & Pringle 1978). The clay consisted of a mixture of Tennessee Ball Clay and Kaolin. Clays containing iron oxides were avoided because they may be toxic. Silica, nepheline, bentonite and whiting were added to the mixture; silica to lower the melting point, nepheline and bentonite as suspension agents, and whiting as a coloring agent. Upon firing the clay turned a flat white providing a reflective rather than a heat-absorbing surface. Clay was rolled out in 1 cm thick slabs, cut into 5 cm \times 5 cm squares and allowed to dry to a leathery consistency. Holes (0.5 cm) were drilled through the centers of the squares which were then fired at 983°C (Cone 8). The chips had a water-holding

capacity of 21 %, determined by drying for 48 h, boiling in distilled water for 2 h to remove air, soaking for 24 h, weighing and drying to a constant weight at 60°C.

The surfaces of some pottery chips (Expt 4) were modified to simulate natural surfaces and provide refuges for zygotes and germlings. One half of the unfired clay surface was imprinted with a nylon mesh netting while the other half was imprinted with #50 grade sandpaper. This technique created 4 microhabitats: vertical and horizontal grooves, flat surfaces, and pits. Approximately 32 squares per chip (flat surfaces, 5 \times 4 mm) were formed by the mesh. The depth and width of the grooves ranged from 0.1 to 0.2 mm and from 0.15 to 0.2 mm, respectively. The grooves were designated vertical (parallel to water flow) and horizontal (perpendicular to water flow); survival was analyzed separately in each. The number and size of the squares and characteristics of the grooves varied slightly because of differential stretching of the nylon and differences in firing and cooling temperatures.

Zygotes were seeded onto pottery chips as follows. Gametes of *Ascophyllum nodosum* are released naturally over a 4 to 6 wk period (April to June) in Maine. Eggs and sperm were obtained by separately forcing release (by drying) of male and female receptacles in shaded trays. Gamete release occurred in 1 to 2 h on mild sunny days, but took considerably longer under cool cloudy conditions. Gametes were collected by rinsing receptacles in beakers containing cool (10 to 15°C) seawater. To initiate fertilization, gametes of each sex were diluted with seawater, combined to produce a dark turbid broth and stirred for 30 s. In the first experiment 15 min was allowed for fertilization. Subsequently a minimum of 30 min was employed. Following fertilization the zygote suspension was further diluted and gently poured over chips in shallow pans. The chips were covered by 1 cm of the suspension and left undisturbed. The pans were shaded and covered with aluminum foil to prevent warming and enhance germination. After the prescribed setting time, the solution was carefully siphoned from the pans to minimize disturbance. The chips were randomized, gently removed from the pans, subjected to wave or water movement and then placed in moist, covered pans until sampled. Zygotes were regularly misted (fine spray) with cold seawater to prevent desiccation until censusing was complete.

Zygotes in Expts 1, 2, and 3 were counted by first estimating densities of entire chips as light, medium and heavy, and then by random subsampling using eyepiece grids. In Expt 4, zygotes were counted on 18 squares (flats) on light density chips (< 20 per flat). On medium density chips (21 to 200 per flat), zygotes were counted on 6 randomly selected flat squares. For high

density chips (> 200 per flat), 6 randomly selected flats were subsampled using an eyepiece grid. The number of zygotes in randomly selected horizontal and vertical grooves was estimated and placed into 7 categories: 0, 1–25, 26–50, 51–75, 76–100, 101–125 and > 125 zygotes per groove. Zygotes on the pitted surface were counted in 10 randomly selected pits. Comparisons between and within grooves and pits were difficult because they contained unequal areas and were not easy to quantify. As a result, data for all surfaces were converted to percent survival of control chips. Controls in all experiments consisted of chips handled identically to experimental chips except for the specific treatment.

Expt 1 was designed to simulate the recent settlement of zygotes in the field and to determine the impact of natural (low energy) waves on survival. To simulate the short period available for natural gamete release and zygote attachment during a flooding tide, zygotes were seeded onto chips and allowed to set undisturbed for only 15 min. Chips were randomized and exposed to waves either individually (Trial 1) or as a group by mounting them on plywood strips (Trial 2). The individual chips or strips were hand-held, appressed to the rock surface, and subjected to 6 (Trial 2) or 8 (Trial 1) different wave treatments at Pemaquid Pt (see Fig. 1). Control chips were maintained in air, but misted with seawater, for the duration of the longest wave series (16) in each trial. This provided a conservative estimate of control levels for chips exposed to fewer waves. Control densities averaged 1228 ± 260 and 270 ± 41 zygotes cm^{-2} (mean \pm SD), respectively, for Trials 1 ($n = 3$) and 2 ($n = 5$).

Expt 2 was designed to simulate the effects of low energy waves on survival. The wavemaker was an 10 l asymmetrical open-topped plexiglas box (one side with an obtuse angle). The box was mounted on cylindrical pivots over a plexiglas tank connected to flowing seawater. As the box filled it became unbalanced and spilled the water, creating a wave 2 to 5 cm high.

Zygotes were seeded onto pottery chips and allowed to attach for 9 different time intervals. After seeding, but before testing, experimental and control chips were maintained in seawater in large shallow pans. At the end of each setting period 12 chips (3 per treatment) were carefully removed, placed on a rack 35 cm from the wave machine and exposed to a series of 1, 2, 4 or 8 waves. Control densities for the 24 h treatments averaged 1865 ± 43 zygotes cm^{-2} (mean \pm SD, $n = 3$).

Expt 3 was designed to test the influence of low, medium and high zygote densities and different setting times on survivorship. This experiment was conducted in gently moving water to minimize the dominating effect of water movement on other variables. This series was also used to determine if artifacts were

involved in the low survival at long setting times in pilot studies and Expt 2. Zygotes were subjected to 9 setting intervals in 2 series: (a) 0.5, 1, 2, 3 and 4 h and (b) 6, 12, 16, and 24 h. Following settlement, 6 replicated chips were placed in a reciprocal shaker bath at 10°C for 1 min at 68 oscillations min^{-1} . This produced a flow velocity of 6 to 8 cm s^{-1} (determined with a heated-bead thermister flowmeter; Vogel 1981), which resulted in a 1.5 cm overwash of each chip. Although this experiment simulated intertidal water movements, acceleration forces off the sides of the tank could have increased dislodgment of zygotes. Controls for Series (a) and (b) were based on the 4 and 24 h setting times, respectively, and were maintained in calm water at 10°C. Controls for the low, medium and high density treatments averaged, respectively, (mean \pm SD) 53 ± 9 , 448 ± 31 and 5378 ± 1434 zygotes cm^{-2} for Series (a) and 16 ± 2 , 174 ± 41 and 3006 ± 537 zygotes cm^{-2} for Series (b). To test for differences between density treatments, analysis of variance (ANOVA), linear regression and analysis of covariance (ANCOVAR) were employed (Sokal & Rohlf 1981). Log ($n + 1$) transformations were used to equalize the variance.

To test for the possibility that attachment of zygotes was influenced by environmental conditions (long setting times, high zygote densities and bacterial growth), bacteria adhering to zygotes were removed at 1, 4, 7, 11, 15 and 24 h with a sonicator (Branson 2200). Five zygotes per setting time were individually isolated and sonicated for 30 s in sterile seawater. The suspension was plated on 0.1% glucose and tryptone agar, incubated at 10°C for 24 h, and counted.

Expt 4 was designed to test the influence of refuges, setting times and natural water movement on zygote survival at contrasting exposures: Pemaquid Point, an exposed site, and Montsweag Bay, a sheltered estuarine site (Fig. 1). Zygotes from plants collected near Pemaquid Pt were allowed to set on chips mounted on boards. A multifactorial design consisting of 3 wave treatments (1, 10 and 100 waves), 4 microhabitat types (flat, pitted and vertically and horizontally grooved surfaces) and 3 setting times (1, 2 and 4 h) was utilized and replicated 10 times per treatment. Because of the absence of waves at Montsweag Bay, zygotes were immersed at the edge of the water during a flooding tide for 5 s, 2 and 20 min. These periods were equivalent to the times required to complete the 3 wave treatments at Pemaquid Pt. Densities of control chips (100 wave treatment) at Pemaquid Pt averaged 1577 ± 838 , 1715 ± 592 and 860 ± 634 (mean \pm SD, $n = 10$) cm^{-2} for 1, 2 and 4 h setting times, respectively. Control densities at Montsweag Bay (20 min treatment) averaged 1814 ± 1190 , 2062 ± 860 and 3072 ± 1063 ($n = 10$) for the 1, 2 and 4 h treatments. The data were

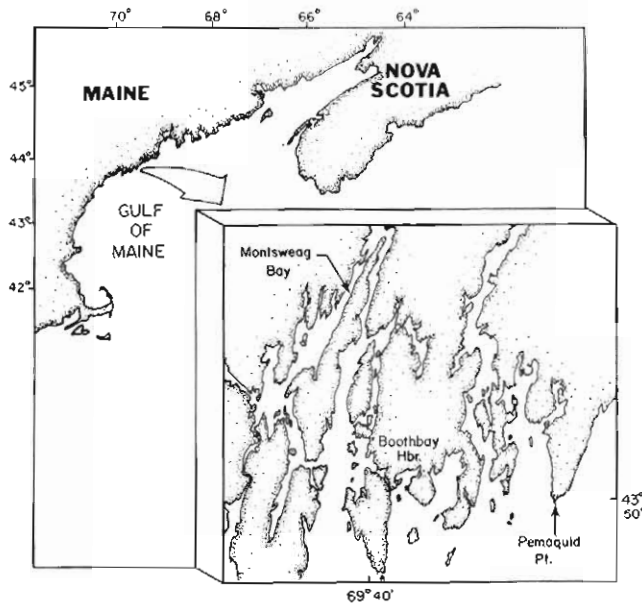


Fig. 1. Location of exposed (Pemaquid Pt) and sheltered (Montsweag Bay) experimental sites

converted to percent (as noted above), transformed with an angular transformation, and analyzed with a 3-way ANOVA.

RESULTS

Expt 1

Zygotes set for 15 min on smooth pottery chips and exposed to natural wave action (20 to 50 cm high waves) showed a classical Type IV survivorship curve (Fig. 2). Approximately 90% of the zygotes were removed by the initial wave in both trials.

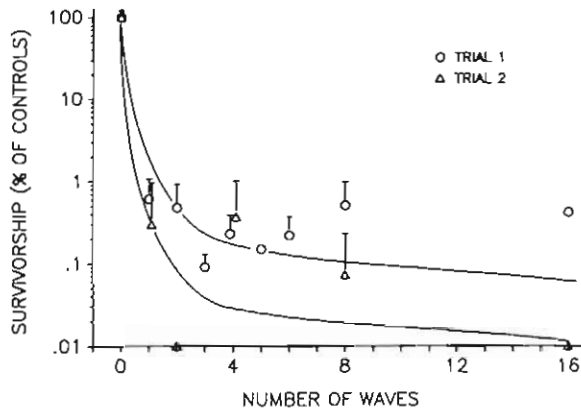


Fig. 2. *Ascophyllum nodosum*. Relative survivorship of zygotes (mean \pm SD) recruited for 15 min and exposed to natural waves at Pemaquid Pt. The absence of error bars indicates that the standard deviation was within the symbol. '0' waves denotes controls

Expt 2

Survival of zygotes, allowed to set over a wide range of times and exposed to artificially generated waves, exhibited a Type IV survivorship curve except at the 3 and 6 h setting times. At the shortest (5 min to 1 h) and longest (12 to 24 h) setting times, survival was reduced. Survival appeared to be enhanced at intermediate setting times and after 1 wave was almost an order of magnitude higher than the other treatments (Fig. 3).

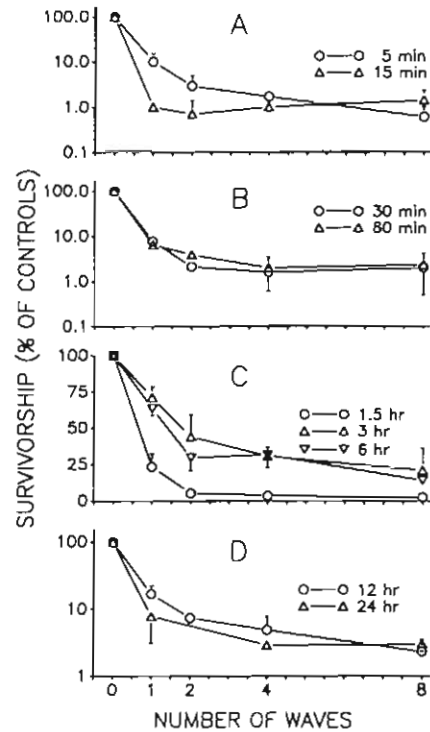
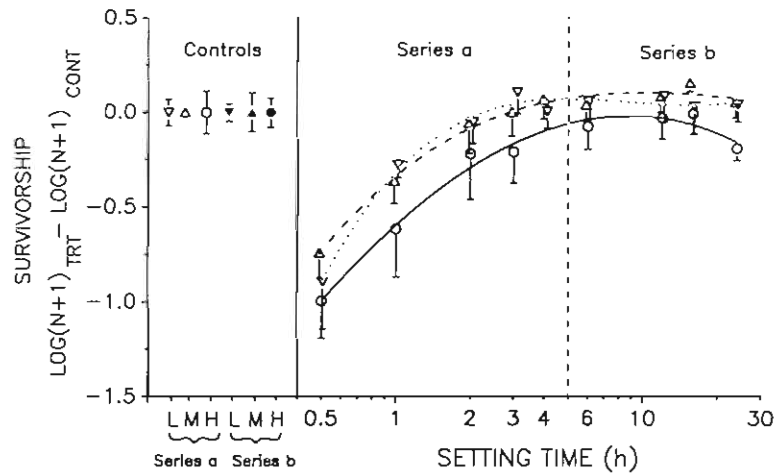


Fig. 3. *Ascophyllum nodosum*. Influence of setting time (A and B = short, C = intermediate, D = long) and waves on relative survivorship of zygotes (mean \pm SD) in a wave tank. '0' waves denotes controls. Note: the y-axes are not the same for each figure

Expt 3

Survival of zygotes exposed to low flow velocities in a shaker bath was positively correlated with setting time up to 3 or 4 h (Fig. 4). Survival of zygotes at 3 to 4 h was equivalent to control treatments (absence of water movement). The 3 density curves in Series (a) fit a cubic polynomial regression line with equal slopes but unequal intercepts. At high density survival of zygotes was significantly lower than at medium and light densities ($p < 0.05$). Survival at low and medium densities for longer setting times was equivalent to

Fig. 4. *Ascophyllum nodosum*. Influence of density and setting times on survivorship of zygotes. Trials conducted under low water movement and in 2 series: (a) 0.5 to 4 h, and (b) 6 to 24 h. Data were log (n + 1) transformed; values shown are means \pm 95% CI. L, M, H denote controls for low, medium and high density after 4 h (Series a) and 24 h (Series b)



controls through 24 h (Fig. 4). However, at high density there was a significant decrease in survival at the longest setting time ($p < 0.05$).

Bacteria isolated from zygotes after 15 h (setting time) in medium and high density treatments ($n = 5$ plates, 6 counts plate⁻¹) produced significantly ($p < 0.05$) more colonies (60.1 ± 29.4 and 44.4 ± 29.1 , mean \pm SD, zygote⁻¹, respectively) than similar isolates from low density cultures (13.9 ± 5.2 , mean \pm SD, colonies zygote⁻¹). Bacteria isolated from shorter treatments (< 15 h) grew at similar rates regardless of zygote density.

Expt 4

Zygotes set for 1, 2 or 4 h on flats or refuges, and exposed to a series of natural waves (20 to 40 cm high) at Pemaquid Pt exhibited Type IV survivorship curves. Regardless of treatment, most recruits were lost with the first wave. Because there were no significant differences ($p < 0.05$) between pits and grooves (one exception; Table 2), these categories were combined for clarity (Fig. 5). Survival was always lowest on the flats and ranged from 7 to 16% after 1 wave and from 1 to 5% after 10 waves. Less than 0.2% survived after 100 waves. Survival in pits and grooves was significantly higher than on flat surfaces for 1 and 10 waves. However, cohorts in these refuges also approached extinction after 100 waves.

Survival of zygotes exposed to a gently flooding tide in Montsweag Bay was substantially higher than at Pemaquid Pt. Survival was again lowest on the flats, ranging from 65 to 100% after 5 s and from 59 to 82% and 27 to 45% after 2 and 20 min, respectively (Fig. 6). Conversely, mortality was almost non-existent in the pits and grooves after 5 s and 2 min. After 20 min, survival in refuges ranged from 80 to 92% in the 1 and 2 h treatments and was 49% in the 4 h treatment.

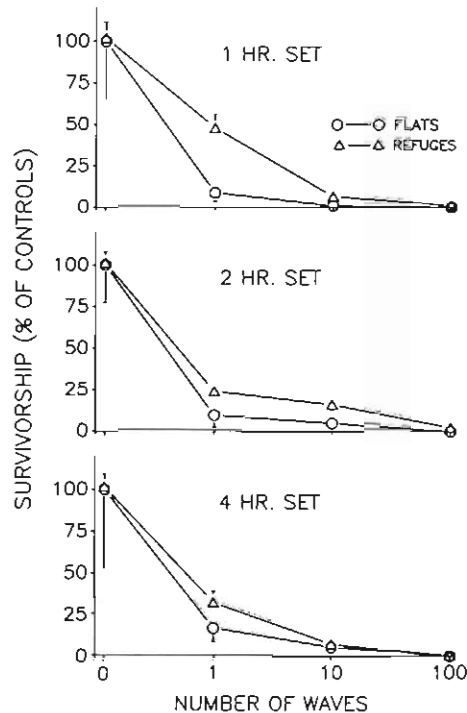


Fig. 5. *Ascophyllum nodosum*. Effects of successive waves, refuges and setting times on relative survivorship of zygotes (mean \pm 95% CI) at Pemaquid Pt. '0' waves denotes controls. Wave amplitudes ranged from 20 to 40 cm during the experiment

At Pemaquid Pt all main effects, except setting time, and all interactions were significant, whereas at Montsweag Bay all main effects and the setting time vs immersion time interaction were significant (3-way ANOVA, $p < 0.05$). Because of the occurrence of significant interaction terms and the dominating influence of waves on survival, the influence of surface texture or setting time upon survivorship were examined at each level of wave (or immersion) exposure (Tables 1 and 2).

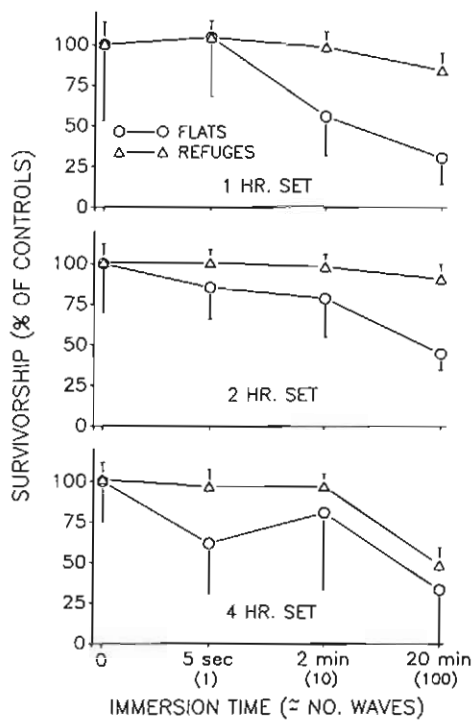


Fig. 6. *Ascophyllum nodosum*. Effects of immersion times (\approx No. waves at Pemaquid Pt), refuges and setting times on relative survivorship of zygotes (mean \pm 95% CI) at Montsweag Bay. '0' waves denotes controls. Water movement was limited to that caused by a gently flooding tide

Significant differences within each level of wave exposure were determined by the Ryan-Elinot-Gabriel-Welsch multiple F test (REGWF) (SAS Institute Inc.

1982). Survival on flat surfaces was significantly different from textured surfaces at each wave treatment and at both sites except for 100 waves at Pemaquid Pt. Significant differences among setting times occurred at Pemaquid Pt but varied in an unordered manner in all wave treatments. This was caused by variation in wave forces, especially in single wave treatments. Such variation was averaged out in multiple wave trials. No significant differences were observed among setting times at the shorter immersion periods in Montsweag Bay. However, after immersion for 20 min zygotes established for 1 and 2 h exhibited better survival ($p < 0.05$) than those set for 4 h.

DISCUSSION

Our results indicate that water motion is a major source of mortality for zygotes of *Ascophyllum nodosum*. Laboratory and field experiments, under relatively benign wave conditions, show that water movement reduces recruitment on protected and exposed shores. Irrespective of setting time and whether or not refuges are provided, 85 to 99% of the zygotes are dislodged by the first 10 waves with most mortality occurring after a single wave. The severity of this disturbance is further accentuated by the virtual loss of entire cohorts within 20 min. Moreover, these estimates of mortality are probably conservative because under natural tidal and water movements the long undisturbed periods required for initial attachment are uncommon. Gametes are usually released at

Table 1. *Ascophyllum nodosum*. Influence of surface texture on survivorship of zygotes at different exposures

Surfaces	Pemaquid Point (Exposed) Mean % survivorship*	Montsweag Bay (Sheltered) Mean % survivorship*
	1 wave	5 s
Horizontal grooves	31.3a	95.2a
Vertical grooves	31.4a	95.3a
Pits	38.9a	96.5a
Flats	9.9b	82.4b
	10 waves	2 min
Horizontal grooves	10.3a	96.9a
Vertical grooves	10.0a	96.0a
Pits	5.4b	92.0a
Flats	2.9c	70.6b
	100 waves	20 min
Horizontal grooves	0.4	83.7a
Vertical grooves	0.4	78.4a
Pits	0.5 ns	67.5a
Flats	0.1	33.1b

* ANOVA with REGWF test on arcsine transformed data; $p = 0.05$, $n = 30$. In each set of 4 entries, values followed by different letters are significantly different

Table 2. *Ascophyllum nodosum*. Influence of setting time on survivorship of zygotes at different exposures

Setting time	Pemaquid Point (Exposed) Mean % survivorship*	Montsweag Bay (Sheltered) Mean % survivorship*
	1 wave	5 s
1 h	35.9a	96.1
2 h	19.5c	94.3 ns
4 h	26.5b	87.9
	10 waves	2 min
1 h	3.7c	88.9
2 h	12.0a	93.4 ns
4 h	5.7b	89.6
	100 waves	20 min
1 h	0.1b	73.5a
2 h	0.7a	79.8a
4 h	0.2b	44.5b

* ANOVA with REGWF test on arcsine transformed data; $p = 0.05$, $n = 40$. In each set of 3 entries, values followed by different letters are significantly different

ebb tide, especially on warm sunny days and are washed free of the receptacles with the incoming tide (Bacon & Vadas unpubl.). Thus, little (motionless) time is available for in situ fertilization and attachment. Hence Expt 1, which shows an extreme Type IV survivorship curve, most closely simulates the conditions found in nature on moderate to wave-exposed shores. These data also indicate that the movement of a flooding tide, except perhaps on highly sheltered shores, e.g. Montsweag Bay, makes attachment of newly formed zygotes extremely difficult.

Survival patterns of zygotes were similar in all experiments despite the wide range of wave treatments and setting times used. The shortest setting times (up to 1.5 h) were consistently least conducive to survival. The reduced survival of zygotes in the 4 h treatment at Montsweag Bay (Expt 4) and the enhanced survival at intermediate setting times (Expt 2) should be noted. The 4 h treatment was run 16 d after the 1 and 2 h treatments, and near the end of the natural release period for *Ascophyllum nodosum* in Maine (zygotes formed from late season gametes appear to be dislodged more easily; Vadas unpubl.). Preliminary studies and Expt 2 indicated that zygotes recruited for the shortest and longest intervals had the highest mortality; intermediate times (2 to 6 h) seemingly provided best survival. However earlier studies indicated that survival should increase with setting time. Charters et al. (1972) showed that carpospores of red algae attached for 19 h were less easily dislodged than those recruited for 7 to 9 h. Similarly, adhesion of germlings of *Sargassum muticum* was enhanced with time (Norton 1983).

Expt 3 clearly demonstrated that attachment or survi-

val was positively correlated with setting time. However, this relationship was confounded by high zygote densities, especially at longer setting times which we infer enhanced bacterial growth. Thus it is possible that bacteria were responsible for the reduced survival at long setting times in Expt 2.

The inability of zygotes of *Ascophyllum nodosum* to adhere quickly and firmly to solid substrata is surprising. Most algae produce mucilage for attachment (Fletcher 1976), but strategies in fucoid algae vary considerably. Zygotes and germlings of *Sargassum muticum* are sticky, sink quickly and attach rapidly (Deysner & Norton 1982). Several fucoids have delayed rhizoidal development and have specialized attachment mechanisms, e.g. mesochiton in *Pelvetia* and special cell walls in zygotes of *Bifurcaria* and *Himanthalia* (Hardy & Moss 1979, Moss 1981). Zygotes of *A. nodosum* and *Fucus* spp. apparently lack stickiness but secrete mucilage through the wall (Moss 1981). Moss (1975) showed that fertilized eggs of *A. nodosum* produce a mucilage pad immediately after settlement which attaches the zygote to the surface. Subsequently a primary rhizoid is produced which secures the germling to the substratum. Under culture conditions rhizoids form within 24 h (Patterson 1986) and are enhanced in darkness (Shedder & Moss 1975). The question of why zygotes of *A. nodosum* do not attach firmly remains unanswered.

Although 2 types of spatial refuges (pits and grooves) were utilized in our studies, neither was effective in moving water. Microhabitat heterogeneity is often considered critical to the survival of intertidal organisms (Bergeron & Bourget 1986). Some species settle in refuges, and gain a foothold on exposed shores, escape

predation, or reduce desiccation and other stresses (Dayton 1971). Refuges for furoid algae generally have been considered escape mechanisms from herbivorous gastropods (Lubchenco 1978, 1983, Schonbeck & Norton 1980, Vadas et al. 1982) which are thought to play a significant role in mortality of juvenile fucoids (Sundene 1973, Vadas et al. 1977, Keser et al. 1981, Lubchenco 1980, 1986). However, refuges may also minimize other disturbances to fucoids. In ice-scoured regions of the North Atlantic *Ascophyllum nodosum* is restricted to crevices and ice-free boulder fields (R. Wilce pers. comm.). In addition, desiccation, light intensity and wave shock pressures (Carstens 1968, Denny 1985b) are reduced in crevices and microhabitats. Survival of germlings of *Sargassum muticum*, for example, is higher in the lee of roughened surfaces (Norton 1983). Our experiments suggest that refuges enhance survivorship of *A. nodosum* in low and moderate energy environments by ameliorating disturbance from water movement. This hypothesis is supported by long-term (1 to 2 yr) survival of germlings in refuges beneath dense canopies on moderately exposed shores (Vadas, Miller & Wright unpubl.).

The inability of a photosynthetic benthic organism to attach readily to natural surfaces cannot be reconciled easily given the dynamic nature of intertidal environments. Life in the littoral zone entails coping with water motion, presumably through evolution. However, *Ascophyllum nodosum* appears to be maladapted to moving water, both in its juvenile stage, as shown here, and possibly in its adult form where high breakage of shoots occurs regularly on exposed and other shores (Vadas 1972, Vadas et al. 1976, 1978). Interestingly, McEachron & Thomas (1987) showed that breaking stress in *A. nodosum* was positively correlated with wave exposure, which suggests that adults are physiologically or genetically adapted to different degrees of wave exposure. It may be unreasonable, however, to expect all life history stages of intertidal organisms to have adapted to water movement. Sea anemones on exposed shores, for example, avoid mainstream velocities (Koehl 1977) and repopulate rocky shores through asexual means (Sebens 1982), thus eliminating 'the need' for specific adaptations by the zygote for dealing with high wave forces.

With *Ascophyllum nodosum* the inability to recruit readily may be compensated by iteroparity and an enormous annual investment in reproduction. *A. nodosum* is a perennial (Baardseth 1970) and, before releasing gametes in the spring invests ca 40 to 50% of its biomass in reproductive structures (Josselyn & Mathieson 1978, Vadas unpubl.). Nonetheless, successful recruitment on exposed and moderately exposed shores probably involves a rare combination of mechanisms or stochastic events. Our experiments and long-

term observations suggest that large new patches are unlikely to develop, except from synchronously recruited cohorts under calm sea conditions lasting for several days. Although modification of wave energy by adult furoid stands is also possible, similar to kelp beds (Jackson & Winant 1983, Tegner 1986), tidally induced water movements probably eliminate all but a trickle of zygotes from recruiting into the understory (Lubchenco 1986, P. Aberg pers. comm., Vadas unpubl.). Episodic recruitment, which is well recognized in many organisms (White 1985) including marine invertebrates (Coe 1956, Vahl 1982, Sebens & Lewis 1985, Tegner 1986) and recently algae (Reed et al. 1988), could account for the presence of *A. nodosum* on moderate and exposed shores. Its presence and repopulation on highly protected shores may be more straightforward (Keser & Larson 1984) although specific mechanisms are lacking.

The ability of *Ascophyllum nodosum* to persist as monocultures on many shores probably results from its perennial habit and the presence of a dense understory of suppressed shoots. Cousens (1986) and Vadas & Wright (1986) have argued that the presence of small relatively unbranched shoots or plants ('juveniles') is the result of competition for light in dense stands rather than persistent recruitment. These suppressed shoots function as 'meristem banks' (Cousens 1985, Vadas & Wright 1986) and are thought to re-establish the bed following disturbance to the canopy. Once established these dense stands or patches of *A. nodosum* appear to occupy space for decades, and thus pre-empt space (Lewis 1976) or outcompete other fucoids for space through growth and longevity (Schonbeck & Norton 1980, Keser & Larson 1984, Cousens 1985, Vadas & Wright 1986).

The absence of *Ascophyllum nodosum* from exposed shores has long been recognized but not explained (Lewis 1964). Lewis (1968) suggested that dispersal may be a problem and noted that sporelings were absent in exposed situations. Our inability to recruit zygotes poured over natural surfaces (Vadas & Wright 1986) indicates that dispersal per se is not the cause of distribution patterns. Similarly, the absence of *A. nodosum* from current swept areas (Lewis 1968, Mathieson et al. 1977, Hardwick-Witman & Mathieson 1983) is probably related to attachment rather than dispersal.

This study provides additional support for the potential importance of recruitment in structuring benthic assemblages (Underwood & Denley 1984, Gaines & Roughgarden 1985). Our data indicate that wave action is an important factor controlling the distribution and abundance of juvenile stages of a dominant species. Although abiotic factors have been neglected in recent decades, they are as important as biotic interactions in determining patterns of abundance (Lewis 1980, Denny et al. 1985, Sebens & Lewis 1985, Underwood 1986). Since *Ascophyllum nodosum* is the dominant life

form on many North Atlantic shores, factors affecting its distribution and abundance may have important ramifications for the structure and organization of rocky intertidal communities.

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LITERATURE CITED

- Baardseth, E. (1970). Synopsis of biological data on knobbed wrack *Ascophyllum nodosum* (Linnaeus) Le Jolis. FAO Fish. Synopsis, No. 38, Rev. 1
- Ballantine, W. J. (1961). A biologically-defined exposure scale for the comparative description of rocky shores. *Fld Stud.* 1: 1-19
- Bergeron, P., Bourget, E. (1986). Shore topography and spatial partitioning of crevice refuges by sessile epibenthos in an ice disturbed environment. *Mar. Ecol. Prog. Ser.* 28: 129-145
- Boney, A. D. (1966). A biology of marine algae. Hutchinson Educational Ltd, London
- Carstens, T. (1968). Wave forces on boundaries and submerged bodies. *Sarsia* 34: 37-60
- Charters, A. C., Neushul, M., Coon, D. A. (1972). Effects of water motion on algal spore attachment. *Proc. Int. Seaweed Symp.* 7: 243-247
- Coe, W. R. (1956). Fluctuations in populations of littoral marine invertebrates. *J. mar. Res.* 16: 212-232
- Connell, J. H. (1961). Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31: 61-104
- Connell, J. H. (1972). Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.* 3: 169-192
- Cousens, R. (1985). Frond size distributions and the effects of the algal canopy on the behaviour of *Ascophyllum nodosum* (L.) Le Jolis. *J. exp. mar. Biol. Ecol.* 92: 231-249
- Cousens, R. (1986). Quantitative reproduction and reproductive effort by stands of the brown alga *Ascophyllum nodosum* (L.) Le Jolis in southeastern Canada. *Estuar. coast. Shelf Sci.* 22: 495-507
- Dalby, D. H., Cowell, E. B., Syratt, W. J., Crothers, J. H. (1978). An exposure scale for marine shores in western Norway. *J. mar. biol. Ass. U.K.* 58: 975-996
- Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-369
- Denny, M. W. (1985a). Water motion. In: Littler, M. M., Littler, D. S. (eds.) *Handbook of phyecological methods IV: ecological field methods: macroalgae*. Cambridge University Press, New York, p. 7-32
- Denny, M. W. (1985b). Wave forces on intertidal organisms: a case study. *Limnol. Oceanogr.* 30: 1171-1187
- Denny, M. W., Daniel, T. L., Koehl, M. A. R. (1985). Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* 55: 69-102
- deVirville, D. (1953). Dépeuplement de la flore marine sur les côtes occidentales du Cotentin. *Proc. Int. Seaweed Symp.* 1: 26-28
- Deysher, L., Norton, T. A. (1982). Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. *J. exp. mar. Biol. Ecol.* 56: 179-195
- Doty, M. S. (1971). Measurement of water movement in reference to benthic algal growth. *Botanica mar.* 14: 32-35
- Fletcher, R. L. (1976). Post-germination attachment mechanisms in marine fouling algae. In: Sharpley, J. M., Kaplan, A. M. (eds.) *Proc. Third Int. Symp. on Biodegradation*. Applied Science Ltd., London, p. 443-464
- Gaines, S., Roughgarden, J. (1985). Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. natl Acad. Sci. U.S.A.* 82: 3707-3711
- Grant, W. S. (1977). High intertidal community organization on a rocky headland in Maine, USA. *Mar. Biol.* 44: 15-25
- Hanic, L. A., Pringle, J. D. (1978). Pottery, a substrate for algal culture. *Br. Phycol. J.* 13: 25-33
- Hardwick-Witman, M. N., Mathieson, A. C. (1983). Intertidal macroalgae and macroinvertebrates: seasonal and spatial abundance patterns along an estuarine gradient. *Estuar. coast. Shelf Sci.* 16: 113-129
- Hardy, F. G., Moss, B. L. (1979). Attachment and development of the zygotes of *Peilvetia canaliculata* (L.) Dcne. et Thur. (Phaeophyceae, Fucales). *Phycologia* 18: 203-212
- Harger, J. R. E. (1970). The effect of wave impact on some aspects of the biology of sea mussels. *Veliger* 12: 401-414
- Jackson, G. A., Winant, C. D. (1983). Effect of a kelp forest on coastal currents. *Cont. Shelf Res.* 2: 75-80
- Jones, W. E., Demetropoulos, A. (1968). Exposure to wave action: measurements of an important ecological parameter on rocky shores on Anglesey. *J. exp. mar. Biol. Ecol.* 2: 46-63
- Josselyn, M. N., Mathieson, A. C. (1978). Contribution of receptacles from the fucoid *Ascophyllum nodosum* to the detrital pool of a north temperate estuary. *Estuaries* 1: 258-261
- Keser, M., Larson, B. R. (1984). Colonization and growth of *Ascophyllum nodosum* (Phaeophyta) in Maine. *J. Phycol.* 20: 83-87
- Keser, M., Vadas, R. L., Larson, B. R. (1981). Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Maine, USA. *Botanica mar.* 24: 29-38
- Koehl, M. A. R. (1977). Effects of sea anemones on the flow forces they encounter. *J. exp. Biol.* 69: 87-105
- Lewis, J. R. (1964). The ecology of rocky shores. English Universities Press, London
- Lewis, J. R. (1968). Water movements and their role in rocky shore ecology. *Sarsia* 34: 13-36
- Lewis, J. R. (1976). The role of physical and biological factors in the distribution and stability of rocky shore communities. In: Keegan, B. F., Deidigh, P. O., Boaden, P. J. (eds.) *Biology of benthic organisms*. Pergamon Press, New York, p. 417-424
- Lewis, J. R. (1986). Objectives in littoral ecology - a personal viewpoint. In: Price, J. J., Irvine, D. E. G., Farnham, W. F. (eds.) *The shore environment*, Vol. 1. Academic Press, New York, p. 1-18
- Lubchenco, J. (1978). Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat.* 112: 23-39

- Lubchenco, J. (1980). Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61: 333–344
- Lubchenco, J. (1983). *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64: 1116–1123
- Lubchenco, J. (1986). Relative importance of competition and predation: early colonization by seaweeds in New England. In: Diamond, J., Case, T. J. (eds.) *Community ecology*. Harper and Row, New York, p. 537–555
- Mathieson, A. C., Tvetter, E., Daly, M., Howard, J. (1977). Marine algal ecology in a New Hampshire tidal rapid. *Botanica mar.* 20: 277–290
- McEachreon, J. C. T., Thomas, M. L. H. (1987). Attachment strength of *Ascophyllum nodosum* (L.) Le Jolis and exposure to wave action. *Botanica mar.* 30: 217–222
- Moss, B. (1975). Attachment of zygotes and germlings of *Ascophyllum nodosum* (L.) Le Jol. (Phaeophyceae, Fucales). *Phycologia* 14: 75–80
- Moss, B. (1981). Attaching mechanisms of zygotes and embryos of the Fucales. *Proc. Int. Seaweed Symp.* 8: 117–124
- Norton, T. A. (1983). The resistance to dislodgement of *Sargassum muticum* germlings under defined hydrodynamic conditions. *J. mar. biol. Ass. U.K.* 63: 181–193
- Oltmanns, F. (1889). Beiträge zur Kenntnis der Fucaceen. *Bibl. bot.* 14: 1–94
- Ortega, S. (1981). Environmental stress, competition and dominance of *Crasostrea virginica* near Beaufort, North Carolina, USA. *Mar. Biol.* 62: 47–56
- Palumbi, S. R. (1984). Measuring intertidal wave forces. *J. exp. mar. Biol. Ecol.* 81: 171–179
- Patterson, B. P. (1986). Ecological relationships between germlings of *Ascophyllum nodosum* (L.) Le Jol. and the herbivorous snail *Littorina littorea* L. M.S. thesis, University of Maine, Orono
- Prntz, H. (1956). Recuperation and recolonization in *Ascophyllum*. *Proc. Int. Seaweed Symp.* 2: 194–197
- Reed, D. C., Laur, D. R., Ebeling, A. W. (1988). Variation in algal dispersal and recruitment: the importance of episodic events. *Ecol. Monogr.* 58: 321–335
- SAS Institute Inc. (1982). SAS user's guide: statistics. SAS Institute Inc., Cary, NC
- Schonbeck, M. W., Norton, T. A. (1980). Factors controlling the lower limits of fucoid algae on the shore. *J. exp. mar. Biol. Ecol.* 43: 131–150
- Schwenke, H. (1971). Water ovement, 2. Plants. In: Kinne, O. (ed.) *Marine ecology*. Vol. 1, Part 2. Wiley, London, p. 1091–1121
- Sebens, K. P. (1982). Asexual reproduction in *Anthopleura elegantissima* (Anthozoa: Actiniaria): seasonality and spatial extent of clones. *Ecology* 63: 434–444
- Sebens, K. P., Lewis, J. R. (1985). Rare events and population structure of the barnacle *Semibalanus cariosus* (Pallas, 1788). *J. exp. mar. Biol. Ecol.* 87: 55–65
- Shedden, A., Moss, B. (1975). Effects of light and temperature on germination and growth of *Ascophyllum nodosum* (L.) Le Jol. *Estuar. coast. mar. Sci.* 3: 125–132
- Sokal, R. R., Rohlf, F. J. (1981). *Biometry*, 2nd edn. W. H. Freeman and Co., New York
- Sousa, W. P. (1984). Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* 65: 1918–1935
- Sundene, O. (1973). Growth and reproduction in *Ascophyllum nodosum* (Phaeophyceae). *Norw. J. Bot.* 20: 249–255
- Tegner, M. J. (1986). Variations in surface currents and recruitment success. In: Thompson, M., Sarojini, R., Nagabhushanam, R. (eds.) *Biology of benthic marine organisms: techniques and methods as applied to the Indian Ocean*. A. A. Balkema, Rotterdam, p. 323–329
- Topinka, J. A., Tucker, L., Korjef, W. (1981). The distribution of fucoid macroalgal biomass along central coastal Maine. *Botanica mar.* 24: 311–319
- Underwood, A. J. (1986). Physical factors and biological interactions: the necessity and nature of ecological experiments. In: Moore, P. G., Seed, R. (eds.) *The ecology of rocky coasts*. Columbia Univ. Press, New York, p. 372–390
- Underwood, A. J., Denley, E. J. (1984). Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong, D. R., Simberloff, D., Abele, L. G., Thistle, A. B. (eds.) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, p. 151–180
- Vadas, R. L. (1972). Marine algae. In: Third annual report, Maine Yankee Atomic Power company, Augusta, Maine, p. 250–310
- Vadas, R. L. (1979). Seaweeds: an overview; ecological and economic importance. *Experientia* 35: 429–432
- Vadas, R. L., Keser, M., Larson, B. (1978). Effects of reduced temperatures on previously stressed populations of an intertidal alga. In: Thorpe, J. H., Gibbons, J. W. (eds.) *Energy and environmental stress in aquatic systems*. DOE Symposium Series (Conf-771114, NTIS), Augusta, Georgia, p. 434–451
- Vadas, R. L., Keser, M., Larson, B., Grant, W. S. (1977). Influence of *Littorina littorea* on algal zonation. *Proc. Int. Seaweed Symp.* 12: 84
- Vadas, R. L., Keser, M., Rusanowski, P. C. (1976). Influence of thermal loading on the ecology of intertidal algae. In: Esch, G. W., McFarlane, R. W. (eds.) *Thermal ecology II*. ERDA Symposium Series (Conf-750425, NTIS), Augusta, Georgia, p. 202–212
- Vadas, R. L., Miller, S. L., Bolis, C. M., Bacon, L., Wright, W. (1982). Population dynamics of *Ascophyllum nodosum*: factors influencing recruitment and germlings. 1st Int. Phycol. Cong., Memorial University St. Johns, Newfoundland, Canada, p. 51
- Vadas, R. L., Wright, W. A. (1986). Recruitment, growth and management of *Ascophyllum nodosum*. *Actas II Congr. Algas mar. chil.* 2: 101–113
- Vahl, O. (1982). Long-term variations in recruitment of the Iceland scallop *Chlamys islandica* from Northern Norway. *Neth. J. Sea Res.* 16: 80–87
- Velmirov, B. (1983). Succession in a kelp bed ecosystem; clearing of primary substrate by wave-induced kelp sweeping. *Oceanologica Acta No SP* p. 201–206
- Vogel, S. (1981). *Life in moving fluids, the physical biology of flow*. Princeton Univ. Press, Princeton
- Watson, D. C., Norton, T. A. (1985). Dietary preferences of the common periwinkle, *Littorina littorea* (L.) *J. exp. mar. Biol. Ecol.* 88: 193–211
- White, A. S. (1985). Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* 66: 589–594