Natural variability in zygote dispersal of *Ascophyllum nodosum* at small spatial scales

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Summary

1. Dispersal of propagules of marine benthic species may contribute to variation in the structure and dynamics of populations. *Ascophyllum nodosum* dominates the mid-intertidal zone of sheltered rocky shores in the north-west Atlantic, and populations often consist of large, mature individuals and few newly recruited thalli.

2. We investigated the dispersal of zygotes of *A. nodosum* at three sites on Swans Island, ME, USA, to determine its variability under natural conditions and to test whether limited dispersal explains recruitment patterns.

3. At each site we released artificially fertilized, marked zygotes from a single point during the rising tide, and sampled their dispersal using two methods: sampling the water column to track the dispersing cloud of zygotes; and assaying caged ceramic tiles affixed to the shore for the presence of marked zygotes.

4. At all sites, zygotes were diluted to ≤1·3% of the initial concentration within 8–12 min of their release. The mean direction of transport was correlated with both wind and tidal current direction at only one site. The most dense settlement occurred at this site, suggesting greater local reproductive success.

5. Regression analyses based on settlement densities suggest that a quadratic model fit the data best for all sites. Quadratic terms occurred in the direction normal to flow, and are interpreted to represent turbulent transport and diffusion. Both linear and quadratic terms were significant parallel to flow, and we ascribe these to advective transport without and with turbulent mixing, respectively.

6. The range of zygote dispersal exceeded 6 m from the source, and therefore cannot explain the exponential decline of recruits in large patches (≈10 m diameter) within adult stands of *A. nodosum*.

7. Migration of zygotes between populations is unlikely, but their local dispersal may strongly influence the spatial and temporal dynamics within populations.

Key-words: Algae, intertidal zone, marine benthic ecology, settlement

Functional Ecology (2001) **15**, 595–604

Introduction

The reproductive stages of many sessile species disperse passively, and the distance and direction travelled by a propagule are determined by its size, shape and density, and the density, viscosity, turbulence and velocity of the fluid medium (Denny & Shibata 1989; McNair, Newbold & Hart 1997). In the case of many terrestrial plant species, seeds are relatively 'heavy', and the distance travelled by dispersed seeds tends to be distributed exponentially even though the range of variation in propagule characters and the average dispersal distances vary considerably across species (Harper 1977; Greene & Johnson 1996; Laman 1996; McGuinness 1997; Ezoe 1998; Sakai, Kukuzawa & Umeki 1998). For example, large, heavy seeds such as acorns (which fall within a few metres of their source) and light and morphologically specialized seeds such as those of dandelions (which can disperse far from their source) show an exponential decline in density with distance from the parent plant.

In contrast to terrestrial plants, the picture is much more complex for the propagules of marine benthic organisms. Seawater is a denser, more dynamically viscous medium than air, and marine spores, eggs,

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zygotes and larvae – which are usually very small (10–100 μm in diameter) – tend to be more buoyant than terrestrial plant propagules and are typically motile. For marine invertebrates, generalizations about dispersal are further complicated by variations among taxa in spawning behaviour and competency for immediate settlement (Pechenik, Rittschof & Schmidt 1993; Pechenik 1999). Given the characteristics of seawater and marine propagules, one might expect propagules of sessile marine organisms to disperse widely in all but the calmest waters.

Yet the evidence from studies of marine macroalgae suggests that dispersal distances are of the order of metres (Anderson & North 1966; Dayton 1973; Paine 1979; Deysher & Norton 1982; Kendrick & Walker 1991; Lu & Williams 1994; Williams & DiFiori 1996, Coyer, Olsen & Stam 1997; Serrão *et al.* 1997), except during storms (Reed, Laur & Ebeling 1988). For example, the dispersal range of fucoid zygotes, in general, is thought to be about 30 m (Chapman 1995), and typically less than 10 m (Lu & Williams 1994; Williams & DiFiori 1996; Serrão *et al.* 1997). Most developing embryos of *Sargassum spinuligerum* disperse less than 1 m (Kendrick & Walker 1991). Short dispersal can be explained by turbulent transport in the direction normal to the substrate bringing propagules rapidly to the bottom (Denny & Shibata 1989; McNair, Newbold & Hart 1997). This also suggests that dispersal distance should be highly variable, although we know of no study that has examined this potential variability.

To examine average dispersal distance and its variability, we studied the fucoid brown alga *Ascophyllum nodosum* (L.) LeJolis (Class: Phaeophyceae). *Ascophyllum nodosum* is the most abundant organism (in biomass) on sheltered shorelines in Maine and elsewhere in the North Atlantic (Vadas & Elner 1992). Populations consist primarily of large, mature individuals (up to 2 m in length). Juveniles (<1·5 years old) are rare (Oltmanns 1889; deVirville 1953; Printz 1956; Boney 1966; Baardseth 1970; Vadas, Wright & Miller 1990), despite a tremendous annual investment in reproduction ($\approx 2·5 \times 10^9$ eggs m^{-2}; Åberg 1996; Åberg & Pavia 1997). This begs questions about the dispersal and fate of *A. nodosum* zygotes. At one particularly wave-exposed location, >99% of the *A. nodosum* zygotes recovered within 36 m of a point source were within 8 m of the source, and 89% were within 1 m (R.L.V., unpublished results). On sheltered shores dominated by *A. nodosum*, dispersal patterns of zygotes are unknown.

Based on previous work, we predicted that dispersal of *A. nodosum* zygotes would be extremely limited on sheltered shores. We further expected dispersal patterns to vary from site to site due to local wind, hydrodynamic and topographic conditions. Recruitment patterns of *A. nodosum* are consistent with a hypothesis of extremely limited dispersal of zygotes. Recruitment of 2-month-old germlings into experimental clearings in *A. nodosum* stands showed an exponential decline with distance from the edge (Dudgeon & Petraitis 2001). This result was consistent across 12 sites. Differences between sites explained less than 10% of the total variation in recruitment. It is unclear, however, if the pattern of recruitment is due to limited dispersal or massive pre- and post-settlement mortality. Thus an additional objective of this study was to determine if limited dispersal could explain the pattern of recruitment observed by Dudgeon & Petraitis (2001).

Ascophyllum nodosum is a tractable experimental model for locally dispersing marine species. *Ascophyllum nodosum* is dioecious, and fertile males and females are easily distinguished by colour. Females release oogonia (packs of four eggs) that disintegrate, freeing individual eggs. Fertilization is external and there is no planktonic stage: oogonia, eggs and zygotes are all nonmotile and negatively buoyant. Zygotes develop a mucopolysaccharide wall following fertilization that can be stained to mark individuals. Our approach was to characterize the dispersal of zygotes, rather than eggs or sperm, by employing a mark–recapture method of large numbers of artificially fertilized, tagged zygotes released from a single point.

Materials and methods

STUDY SITES

Experiments were conducted at three wave-sheltered sites on Swans Island, ME, USA (44°10′ N, 68°25′ W): The Nubble, Pole 24, and Grace. All sites have gently sloping, smooth granite bedrock in the mid-intertidal zone, supporting large stands of *A. nodosum*.

CHARACTERIZATION OF *A. NODOSUM* STANDS: DENSITY, SEX RATIO AND BIOMASS

To estimate the density and sex ratio of *A. nodosum*, we established several transects perpendicular to the shoreline, spanning the mid-intertidal algal zone at each site. Transects at each site were parallel to each other and 5–10 m apart: four transects were sampled at The Nubble and Pole 24, and three at Grace. Two randomly chosen 0·25 m^2 quadrats were sampled at four locations (1, 4, 7 and 10 m from the upper limit of *A. nodosum*) along each transect. All fronds arising from a holdfast were assumed to belong to a single individual. The number of holdfasts in each quadrat was counted to estimate density. The sex of each plant bearing receptacles was determined from the colour of gametes in the conceptacles. Biomass of individual thalli (defined as kg per holdfast) was estimated by weighing 20 randomly chosen thalli from the middle of the *Ascophyllum* bed (approximately +1 m above mean low water) at each site.

Density data were analysed using a pure model II ANOVA of site, transect nested within site, and location crossed with site. Data were square root (+0·5)-transformed prior to analysis, to normalize their

distributions and homogenize variances. Variance components were calculated using the restricted maximum-likelihood method (see VARCOMP procedure in SAS Institute 1989). Based on data from previous experiments, the power of this sampling design to detect a difference of four thalli per square metre was 0·41. A replicated goodness-of-fit G-test was used to test the extrinsic null hypothesis of a 1 : 1 ratio of males and females at each site, and if the sites were homogeneous with respect to sex ratio. Data for biomass were analysed using a one-way ANOVA. The power of the sampling intensity to resolve differences of an average of 0·1 kg per thallus among sites was 0·05.

DISPERSAL EXPERIMENT

The dispersal of zygotes at these three sites was tested on different days during 1997 (Nubble, May 6; Pole 24, May 7; Grace, May 9). At each site we deployed artificial substrates for one tidal cycle in a radial pattern at distances from 1–6 m about a central source point (hereafter, origin). Substrates were $5 \times 5 \times 1$ cm white ceramic tiles with a screw hole in the centre (Vadas *et al.* 1990). The tiles were imprinted with a very fine-grain sandpaper (#220) that mimicked the pits of natural surfaces, and scored with a grid of $0·5 \times 0·5$ cm squares. Tiles were caged in nylon window screen (1·5 mm mesh size) to protect them from herbivores. The cage was held above the surface of the tile by a spacer consisting of a plastic washer atop a stiff wire (≈ 2 cm long), covered with tygon tubing, attached to the screw in the tile's centre. Tiles were screwed into plastic anchors in holes drilled in the rock. We assume that the cages do not differ in the permeability of the mesh to zygotes at the different flow speeds observed.

For placement of the tiles, we divided each site into four quadrants; upslope, downslope, and left and right alongshore of the origin (Fig. 1). Eight tiles (two replicates in each of the four quadrants) were deployed at 2, 3, 4, 5 and 6 m from the origin. Four tiles (one in each quadrant) were placed at the 1 m radius. The four tiles on the 1 m radius were placed (relative to the shoreline) directly upslope, downslope, left and right of the origin. The chord distance between these tiles along a 1 m radius is 1·414 m, and this chord distance was conserved for the replicate tiles placed at radii from 2–6 m from the origin, so that the spatial scale of replication was constant for every distance sampled. Placement was determined in the following way. Eight tiles along a circle of 2 m radius and separated by a chord distance of 1·41 m are spaced 45° apart. So we placed tiles on a polar coordinate system at 22·5, 67·5, 112·5, 157·5, 202·5, 247·5, 292·5 and 337·5°, such that pairs of replicates were centred within each quadrant. For the 3–6 m radii, we randomly selected an angle within each quadrant that served as the mid-point in the arc between the two replicate tiles, which were constrained to be a chord distance of 1·41 m apart and both in the same quadrant.
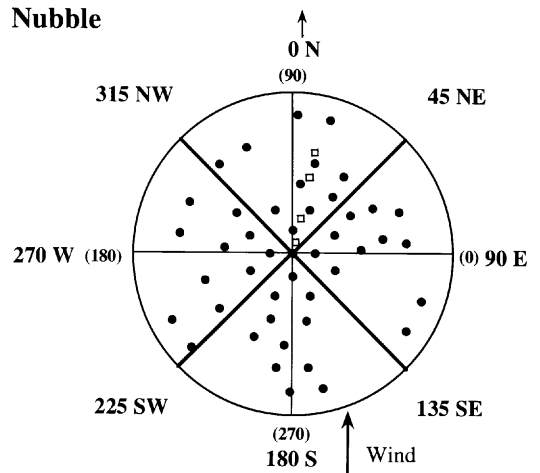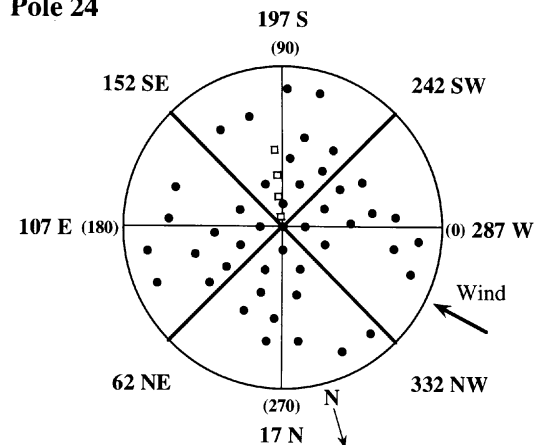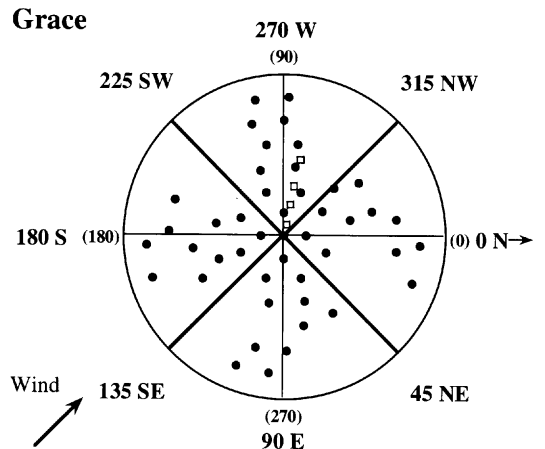

Fig. 1. Schematic diagram illustrating the radial array of tiles deployed within the four quadrants at each site. Quadrants indicated by thick diagonal lines intersecting at the origin. Locations of tiles represented by solid circles. Positions of clamp stands with mounted syringes for samples of the water column are represented by open squares. Compass headings in degrees with respect to the origin at each site are indicated around the periphery of each plot. Small numbers in parentheses along the abcissa and ordinate of each plot represent the angle in the polar coordinate system. For each plot the top (90° in polar coordinates) represents the upshore direction, and the bottom (270°) points seaward. Small arrows indicate magnetic north; large, thicker arrows point in the direction from which the wind blew on the day of the experiment at each site. Compass headings in magnetic north deviate from true north by 18°23′ W.

Zygotes of *A. nodosum* were produced by large-scale artificial fertilizations. We collected fertile male and female fronds of *A. nodosum* on the afternoon prior to each release, and kept them isolated until fertilization. Fronds of each sex were spread out in stainless steel trays, covered with damp paper towel, and left overnight (≈6–8 h) to mimic emersion during low tide. The following morning, fronds were rinsed in 2–3 l seawater to remove gametes on the surface of receptacles. The suspensions of sperm and eggs were filtered through 200 µm mesh to remove debris. The suspension of sperm was added to the suspension of eggs and mixed thoroughly to initiate fertilization.

Artificially fertilized zygotes were tagged with calcofluor white (Sigma Chemical Co., St Louis, MO, USA), a fluorescent stain which binds to cell walls. This stained developing zygotes, but not unfertilized eggs which lack cell walls. Staining allowed us to distinguish artificially released zygotes from naturally released zygotes. As the negatively buoyant zygotes settled, the volume of seawater in the fertilization bucket was siphoned down to ≈4 l (≈10–15 min after initiating fertilization). A 1 l solution of calcofluor white in seawater (0·7 g l^{-1}) was then added to the zygote suspension and mixed thoroughly (final concentration 0·13 g l^{-1}). Fertilization and staining were allowed to continue for a total of 60 min (except for Pole 24, where total time was reduced to 23 min because of bad weather that affected the tide).

Five 5 ml samples were pipetted from the zygote bucket into plastic vials containing 5 ml buffered formalin (final formalin concentration, 2·5%) to determine, from the average of these samples, the initial concentration of zygotes that were released. For each, 1 ml subsamples were counted using a Sedgewick Rafter counting slide. Zygotes were counted in six randomly chosen fields across the slide consisting of nine squares each. The average for each subsample was estimated from the zygote counts in these 54 squares.

Immediately prior to release of the zygotes, we released a stream of dye at the surface above the origin to determine the direction (compass heading) of the bulk flow of water. Based on the direction of the bulk flow, two clamp stands were set out, in line with the bulk flow and a known distance apart. A second dye stream was then released, and the time it took for the centre of the cloud of dye to travel between the clamp stands was recorded and used to estimate flow speed.

The method for release of zygotes was intended to mimic the natural release of *A. nodosum* gametes. In nature, sperm and eggs released from conceptacles during low tide are washed off the receptacles in the flooding tide. Artificial fertilizations were timed such that release of stained zygotes coincided with complete, or nearly complete, inundation of the site by the incoming tide. The zygote suspension was poured into a funnel, down a ≈1·5 m length of garden hose and out through an attached garden sprinkler. The suspension of zygotes dribbled out of the sprinkler head into the water ≈10 cm above the bedrock. The time to drain the

zygote solution was 2·5 min at The Nubble, and 7 min each at Pole 24 and Grace. During the release, water depth at the origin was ≈20–60 cm.

Ascophyllum nodosum zygotes in the water column were sampled following release to characterize their dilution and transport. Clamp stands with two 10 ml syringes attached 10 cm above the base were placed as described above, in the direction of the flooding tide. The direction of the flood tide was displaced 10° right, 5° left, and 10° right at The Nubble, Pole 24 and Grace, respectively, from the compass heading of directly upslope. One syringe at each point was filled immediately on completion of zygote release, and the second was sampled 5 min later. The samples were preserved by injecting them into a plastic vial containing 5 ml buffered 5% formalin. Zygote concentrations for each distance and time sample were estimated from the average of three 1 ml subsamples, counted using a Sedgewick Rafter counting slide. Naturally and artificially released zygotes were distinguished by epifluorescence. For Grace and Pole 24, counts of each subsample were based on all 1000 squares (1 ml) of the slide. Counts from The Nubble are based on 200 squares (200 µl) per subsample.

Tiles were collected during the subsequent low tide and placed in boxes lined with damp paper towels. Tiles and preserved water column samples were transported to the University of Maine at Orono and held in the dark at 5 °C. Settled zygotes of *A. nodosum* were counted by viewing tiles on an inverted microscope at 63× magnification. Under UV light, naturally fertilized zygotes autofluoresce red and Calcofluor white zygotes fluoresce blue. Both red and blue zygotes were counted in five 0·5 × 0·5 cm squares on each tile. Only counts of experimentally released (blue) zygotes are reported here. The average of the five squares was used to estimate the average zygote density for each tile.

ANALYSIS OF DIRECTIONALITY

For tests of directional dispersal, data for each site were grouped into four equal-length arcs that corresponded to the four quadrants of the experimental site in the intertidal zone. The mean vector length and angle of zygote dispersal for each site were determined according to the method described by Batschelet (1981) for grouped data. Data for Pole 24 were bimodal, so all angles for this site were doubled prior to analysis to obtain a unimodal sample (Batschelet 1981). The *V*-test was used to test whether dispersal patterns at each site were directional against a null hypothesis of randomness. This test is modified from Rayleigh's test to include an expected direction of movement, and a component, ν, that represents the projection of the observed mean vector onto the hypothesized direction. Values of ν range from −1 to +1, with values near +1 indicating a close association between observed and expected directions, whereas smaller values reflect a poor association. For each site, two *V*-tests were

performed. One tested whether any directionality in dispersal was associated with the prevailing wind direction; the other tested if dispersal was associated with the direction of the flooding tide.

REGRESSION ANALYSIS OF DISPERSAL PATTERN

Regression analysis was used to fit descriptive models to the settlement of *A. nodosum* zygotes. The objective of this analysis was to evaluate whether the general form of the regression model was similar among sites. An *a priori* decision was made to use sequential regression methods but to limit the models to quadratic equations which can completely describe simple diffusion models. The dependent variable was the average number of zygotes per 0.25 cm^2. The independent variables were the linear and quadratic terms based on the X, Y coordinates of each tile (X axis = along shore; Y axis = low to high in the intertidal zone). Forward selection, backward elimination and maximum R^2 procedures were used to search for the simplest model that explained most of the variation. Default values in SAS (Statistical Analysis System version 7, SAS Institute, Cary, NC, USA) were used in the selection procedures. Selection of independent variables was performed hierarchically; for example, a quadratic term could not be added to the model until all related linear terms had been added.

Evaluating whether the general form of the model applied regardless of site is, in effect, using regression as a diagnostic tool for parameter estimation, not a test of a hypothesis that dispersal differs among sites. The analysis sought to estimate the magnitude, sign and significance of each estimated parameter at the three sites. Initial analyses yielded different parameter estimates between sites, but these estimates had very large standard errors, suggesting that the estimates were unduly affected by a few observations (high leverage – or influence – points, or outliers). Failing to compare model estimates with and without these points can lead to the inference that the form of model differed between sites, when in fact the differences were driven by outliers exerting leverage in each data set. Therefore outliers were deleted prior to fitting response surfaces using the methods and guidelines suggested by Belsley, Kuh & Welsch (1980) and Myers (1990). We report the results of analyses based on the complete data sets and data sets with outliers removed.

Results

CHARACTERISTICS OF *ASCOPHYLLUM* STANDS AT EACH SITE

The population structure of *A. nodosum* was similar among the three sites, with no difference in the density of thalli among sites (19.9 ± 2.0, 16.0 ± 1.7 and 34.8 ± 7.9 for Nubble, Pole 24 and Grace, respectively; $F_{2,17} = 1.04$, $P = 0.37$, MSE = 2511.05). However, densities varied with tidal height differently among the three sites ($F_{site \times height(6,24)} = 4.53$, $P < 0.01$, MSE = 536.85). Most of the variation in density of thalli was associated with small-scale patchiness at the scale of tidal elevation and different locations (≤ 5 m) within a tidal elevation. Differences in average biomass per plant among sites were not sufficient to reject the null hypothesis ($F_{2,57} = 0.78$, $P = 0.47$, MSE = 0.283). The sex ratio of *A. nodosum* at each site was $\approx 1 : 1$ (M : F ratios: Nubble, 48 : 50; Pole 24, 43 : 48; Grace, 45 : 40; $G_{1:1} = 0.03$, df = 1, $P > 0.5$; $G_{homogeneity} = 0.58$, df = 2, $P > 0.5$).

ANALYSIS OF DIRECTIONALITY

Wind conditions and surface-water velocities of the flooding tide differed among sites. At The Nubble [compass bearing up (or down), intertidal zone relative to magnetic north (hereafter, aspect) = 180°], a southerly wind blew upslope and velocity was ≈ 9.4 cm s^{-1} along a compass heading of 10° N. At Pole 24 (aspect = 17°), a north-west wind prevailed and the surface water velocity of the flooding tide was ≈ 3.5 cm s^{-1} along a compass bearing of 192° S. Flow was slowest at Grace (aspect = 90°) where the velocity of the flooding tide under a south-easterly breeze was ≈ 0.5 cm s^{-1} along a compass bearing of 280° W.

Similar quantities of zygotes were released at each site, with slightly fewer released at Grace (Table 1). Immediately after release, the highest concentration of zygotes in the water column was found at 0.5 m from the origin at all three sites (Fig. 2). Dilution was rapid. The zygote concentration estimated at 0.5 m at The Nubble (2.8×10^5 l^{-1}) corresponded to 4% of the suspension released, and the zygotes sampled at the other sites were even more dilute. At sites other than The Nubble, higher concentrations of zygotes were found further from the origin in samples taken immediately after release. For instance, at Grace zygote concentrations exceeded 2.4×10^4 l^{-1} at 1.0 m from the origin.

Five minutes after release, the distributions of zygotes dispersing in the direction of advection were similar between the three sites. The greatest concentrations of zygotes were observed at 1.5–2.0 m from the

Table 1. Number of zygotes released from artificial fertilizations and estimated percentage of total released that settled in the study area (based on average per quadrant at each radius and the corresponding area of the arc in a quadrant). Average estimate is based on $n = 5$ samples

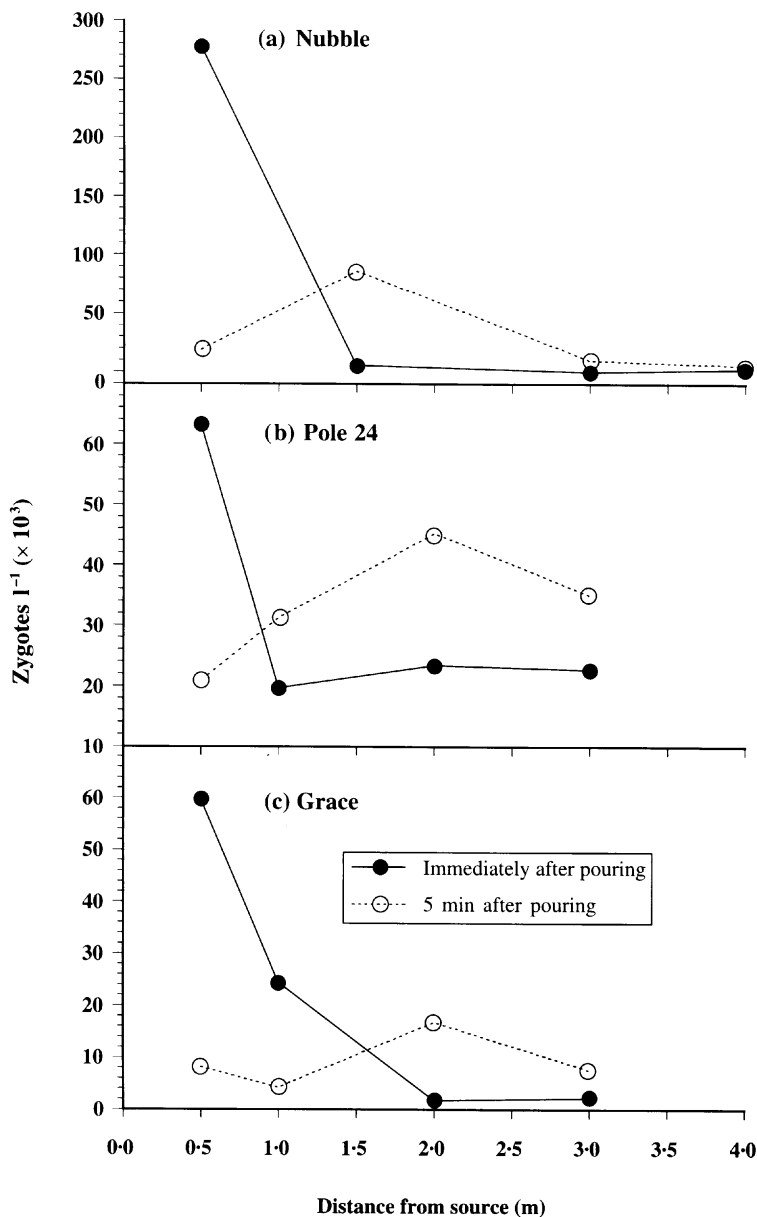| Site	Estimated zygote number	Percentage in study area
The Nubble	3.54×10^7	1.83
Pole 24	2.88×10^7	2.01
Grace	1.64×10^7	42.87

Fig. 2. Concentration of zygotes of *A. nodosum* sampled at different distances from the origin at (a) The Nubble; (b) Pole 24; (c) Grace immediately after completing release (●) and again 5 min later (○). Values represent the average of three 1 ml subsamples of one sample at each location.

Fig. 3. Average densities of zygotes of *A. nodosum* settled at (a) The Nubble; (b) Pole 24; (c) Grace. Each tile is plotted according to its *x* (along-shore) and *y* (up-shore) coordinates on the shore; the *z* axis represents zygote density. Axes are oriented such that positive *y* values refer to up-shore from the origin.

origin, and these concentrations corresponded to 0·6–1·2% of the zygote concentration released. At Pole 24, the concentrations of zygotes exceeded $2·0 \times 10^4$ zygotes l^{-1} at all distances.

Average settlement densities on tiles were similar at The Nubble and Pole 24 (≈ 9 cm^{-2}), but were an order of magnitude greater at Grace than at the other two sites ($F_{site2,9} = 7·08$, $P < 0·025$, MSE = 891·504; Fig. 3). Interestingly, Grace was the site where the fewest tagged zygotes were released (Table 1). Approximately 43% of the zygotes released at Grace settled within the 12-m-diameter study area, compared to 1·8 and 2·0% at The Nubble and Pole 24, respectively (Table 1). The average distance dispersed (determined from the frequency of zygotes recaptured on each tile a known
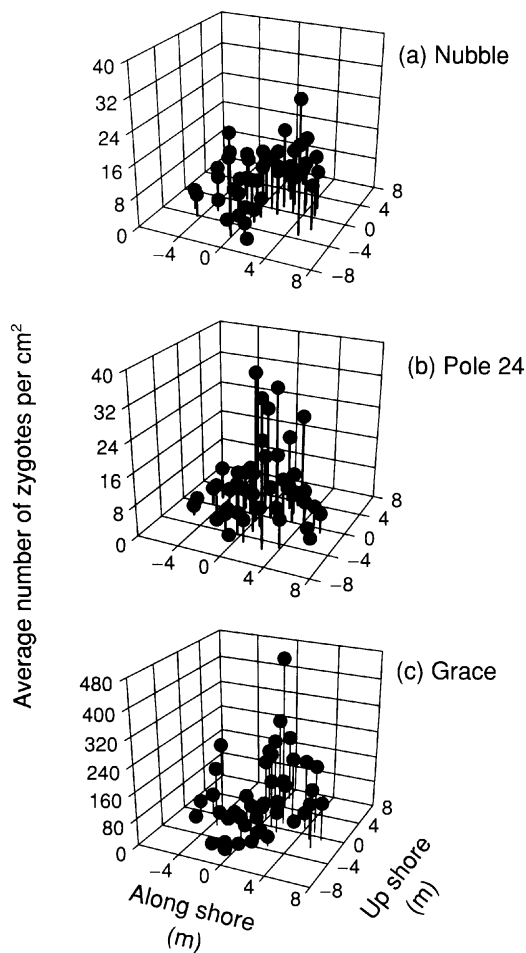
radial distance from the source divided by the total number of zygotes recaptured) was 3·3, 3·7 and 3·8 m at Pole 24, Grace, and The Nubble, respectively.

The average direction of dispersal of zygotes with respect to the prevailing wind and tidal current directions differed between sites. At The Nubble, neither of the hypotheses of directional dispersal associated with wind or current direction was supported by the *V*-test. The length of the average vector, *r*, however, indicated a nonrandom pattern of dispersal when tested without an expected direction of settlement (Rayleigh's test: *n* = 44, *P* = 0·04). The average vector representing the zygote settlement pattern showed a trend for greater settlement to the east of the origin (compass bearing 83·17° E; θ = 6·83°, where θ = the angle on a polar coordinate system oriented with 90° directly up the shore from the origin) along the abcissa (Table 2; Fig. 3). At Pole 24, by contrast, the average direction of zygote settlement was upslope from the origin (compass bearing 198° E; θ = 88·2°) and correlated with the direction of the tidal current, but not with the wind direction. Only at Grace was the average direction of

Table 2. Analyses of directionality of zygote dispersal at three sites. The length and angle of the average vector describing dispersal at each site are represented by r and θ, respectively. Values of r with an asterisk denote significance using Rayleigh's test at $\alpha = 0.05$. $\angle$ refers to the angle of the mean vector for each site converted to a compass direction. R represents the direction of the flood tide vector. v is the correlation between the observed mean direction of dispersal and the direction of wind or water flow. U represents the test statistic of the V-test. Analyses based on $n = 44$ tiles per site

| | | | | | V-test | | | | | |
| | | | | | Wind | | | Current | | |
Site	r	θ (°)	$\angle$ (°)	R (°)	v	U	P	v	U	P
Nubble	0·281*	6·83	83·17 E	10 N	0·033	0·31	>0·10	0·081	0·76	>0·10
Pole 24	0·378*	88·18	198·82 S–SW	192 S–SW	−0·024	−0·22	>0·10	0·354	3·32	<0·001
Grace	0·454*	61·99	298·01 W–NW	280 W	0·434	4·07	<0·001	0·432	4·05	<0·001

Table 3. Regression models describing patterns of zygote dispersal of *A. nodosum* at each site. X = along the shore, Y = low to high in the intertidal zone

| Analyses using all data | | | | | | Analyses excluding outliers | | | | | |
Source	df	SS	F	P	Adj. R^2	Source	df	SS	F	P	Adj. R^2
The Nubble											
Model	5	548·896	2·879	0·02	0·179	Model	5	416·512	7·353	<0·01	0·462
Error	38	1449·024				Error	32	362·544			
Source		Est.	SE	t	P			Est.	SE	t	P
Intercept		8·612	1·600	5·38	<0·01			8·804	0·932	9·43	<0·01
X		1·136	0·344	3·29	<0·01			0·768	0·232	3·32	<0·01
X^2		0·100	0·108	0·92	0·37			0·064	0·076	0·82	0·42
Y		−0·304	0·316	−0·96	0·35			0·468	0·232	2·02	0·05
Y^2		−0·048	0·092	−0·50	0·62			−0·240	0·068	−3·53	<0·01
XY		−0·088	0·144	−0·62	0·54			0·084	0·108	0·77	0·45
Pole 24											
Model	5	816·752	2·755	0·03	0·170	Model	5	442·352	5·343	<0·01	0·358
Error	38	2253·104				Error	34	562·944			
Source		Est.	SE	t	P			Est.	SE	t	P
Intercept		12·332	2·024	6·10	<0·01			8·496	1·172	7·25	<0·01
X		−0·100	0·416	−0·25	0·81			−0·120	0·220	−0·55	0·59
X^2		−0·332	0·120	−2·79	<0·01			−0·172	0·064	−2·67	0·01
Y		0·684	0·424	1·61	0·12			0·824	0·240	3·45	<0·01
Y^2		−0·008	0·128	−0·05	0·96			0·052	0·072	0·70	0·49
XY		−0·352	0·212	−1·67	0·10			−0·132	0·116	−1·13	0·27
Grace											
Model	4	152 661·712	6·088	<0·01	0·321	Model	4	107745·44	11·382	<0·01	0·522
Error	39	244 479·68				Error	34	80466·544			
Source		Est.	SE	t	P			Est.	SE	t	P
Intercept		67·512	20·352	3·32	<0·01			49·508	13·212	3·75	<0·01
X		7·436	4·232	1·76	0·09			9·220	2·696	3·42	<0·01
X^2		1·436	1·200	1·20	0·24			2·092	0·752	2·78	<0·01
Y		18·060	4·132	4·37	<0·01			14·428	2·696	5·35	<0·01
Y^2		1·652	1·196	1·38	0·18			1·372	0·768	1·79	0·08

dispersal correlated with both wind and tidal current directions. The mean vector ($\theta = 61.9$) describing the settlement pattern lay between the wind and tidal current directions.

REGRESSION ANALYSIS OF DISPERSAL PATTERN

The three selection procedures – forward selection, backward elimination and maximum R^2 – usually gave the same result, and a quadratic model had the best fit for settlement patterns at all sites (Table 3). For each site, the estimate of a quadratic component was significant only in one direction (either perpendicular or parallel to the shoreline). At The Nubble and Pole 24, these parameter estimates were negative, indicating reduced settlement with increasing distance from the origin, whereas at Grace the quadratic parameter estimate was positive parallel to the shoreline. Such a parameter indicates greater settlement along the

shoreline at distances further from the origin (within the range of distances we tested). In the direction normal to the 'quadratic' direction, the significant parameter estimates indicate that settlement densities varied linearly. At The Nubble and Pole 24, the parameter estimates indicate shallow positive slopes, meaning gradually increasing settlement density with distance, but at Grace the linear gradient upslope was steep. Models for The Nubble and Pole 24 fit best when an XY term was included (i.e., the pattern in one direction varies depending on position in the direction normal to it), but in both cases no parameter estimates significantly different from zero were detected.

A comparison of model analyses with and without outliers shows that both yielded parameter estimates for model terms that varied between sites. The estimates with outliers omitted had smaller standard errors, providing greater confidence in their estimation. Most of these latter estimates are within one standard error of the estimates from the complete data.

Discussion

We found that our estimated average dispersal distances (3·3, 3·7 and 3·8 m at Pole 24, Grace, and The Nubble, respectively) of *A. nodosum* at each of three sheltered shores on Swans Island were greater than predicted by theory and previous experiments (Dayton 1973; Paine 1979; Denny & Shibata 1989; Kendrick & Walker 1991; Lu & Williams 1994; Williams & DeFiori 1996; Coyer, Olsen & Stam 1997; McNair, Newbold & Hart 1997; Serrão *et al.* 1997). Moreover, these distances must underestimate the true dispersal distance, because ≈57% of the zygotes at Grace and 98% at both Pole 24 and The Nubble dispersed beyond our 12 m diameter study area. These estimates are based on the difference between the number released and the average density of settled zygotes at each radius multiplied by the area of the belt between radii. If settlement density is constant, or increases with distance from the source, the actual number of zygotes that settles over a larger area is greater further from the source (at least in one direction) than nearby. However, along the shoreline or seaward, the number of settlers will increase only up to some distance beyond which it must decrease as zygotes are depleted from the water column.

Most importantly, these data show that the passive dispersal of nonmotile, negatively buoyant propagules in sheltered waters is enormously variable both among and within sites. Average dispersal distances cannot be predicted from flow velocity, because the average vector representing dispersal may not correspond with flow velocity, as occurred at The Nubble. In contrast, tidal current and dispersal vectors were positively correlated at both Pole 24 and Grace. At the latter site, the dispersal vector was correlated with both wind and current vectors, perhaps because the slow flow was influenced more by wind blowing across the surface. We suggest that dispersal distances and directions may be sufficiently variable under natural conditions to make estimates of average dispersal distances meaningless. Such estimates probably are appropriate only in simple unidirectional, laminar flow conditions with featureless bottoms. Few studies (Grosberg & Quinn 1986; Grosberg 1987; Kendrick & Walker 1991) have examined the dispersal of propagules of a marine taxon with 1 m resolution in all directions from a source, and our data suggest that the variability at these small spatial scales warrants equivalent or greater resolution in future studies. The ecological importance of propagule dispersal may lie in the variance of dispersal, rather than the average distance dispersed.

DESCRIPTIVE MODELS OF DISPERSAL

Given the high variability of dispersal, we recommend using descriptive models to characterize the distribution of dispersed propagules of marine taxa. A simple model is unlikely to accommodate dispersal patterns of marine taxa. A single class of regression model containing only linear and quadratic terms was sufficient to explain between approximately 36 and 50% of the variation in dispersal of *A. nodosum* at each site. All sites fit a regression model comprising a significant linear component in one direction and a significant quadratic component in the direction normal to the first. The different parameter estimates of the model for each site may reflect site-specific interactions between hydrodynamics and shore topography. We hypothesize that the linear component corresponds to advection in laminar flow, whereas quadratic components correspond to mixing in the direction parallel to flow and transport by mixing in the direction normal to flow. At Pole 24 and Grace, where flow speeds were slowest, the model indicated that settlement of zygotes increased linearly up the intertidal zone in parallel with the flooding tide. Increased settlement with tidal elevation is consistent with the reproductive behaviour of *A. nodosum* and earlier predictions about the dispersal path of zygotes (Åberg & Pavia 1997).

The slope of the linear term of the model for Grace was an order of magnitude greater than that for the other sites, indicating a much steeper gradient in settlement density across the 12 m diameter experimental array. The slower flow at this site failed to transport as many zygotes beyond the study area before they hit the bottom. Instead, zygotes accumulated at the water line higher in the intertidal zone and were deposited on those tiles furthest from the origin that were near the high water mark of the tidal cycle, and the slow flow probably resulted in less resuspension of settled zygotes. At Pole 24, where flow speed was faster than at Grace, the few settlers in the path of advection suggest that most zygotes were either directly transported, or were resuspended and subsequently transported, to the mudflats in the lower intertidal zone below the study area. There, zygotes were unlikely to survive. At The Nubble, where the flood tide was swiftest,

settlement density declined in a quadratic pattern with distance in the direction parallel to flow. We infer that greater turbulence in the water column associated with faster flow resulted in short residence times for many zygotes that were deposited nearer the origin (Denny & Shibata 1989; McNair, Newbold & Hart 1997). We suggest that turbulence blurred the linear pattern seen at the other sites in the direction of advection.

At Pole 24 and Grace, dispersal varied in a quadratic pattern parallel to the shoreline (normal to the direction of the flooding tide). At Pole 24, like The Nubble, the negative quadratic term indicated reduced settlement with distance from the origin, as is expected where transport is due to mixing. The regression model for Grace contains a positive quadratic term that suggests increasing settlement densities with distance from the origin in the range of distances tested. In contrast, the model for The Nubble shows a significant linear component parallel to the shoreline normal to flow. The positive quadratic term for the Grace model and the linear term for The Nubble model are probably artefacts of the limits of our experimental design. At both sites, most of the recovered zygotes were displaced laterally alongshore as well vertically up and down the shore. Since the maximum radius sampled was 6 m from the origin, our design could not detect a peak settlement radius, nor any subsequent decline in settlement at the distance along the shoreline where the supply of zygotes in the water column becomes depleted. A wider range of distances sampled along the shore at these sites would have resulted in negative quadratic terms normal to flow.

CONSEQUENCES OF VARIABLE DISPERSAL

At all sites, many zygotes dispersed beyond 5 m. Whether zygotes of *A. nodosum* disperse locally or leave a population is really a matter of scale. On many sheltered shores dominated by *A. nodosum*, the substrate below the mid-intertidal zone is a mosaic of rock and mud, so zygotes dispersing only 5–10 m effectively may be lost from the population after settling on mud and dying. Even at the most sheltered sites, most zygotes can be lost from the source population, thereby contributing to the few recruits observed in populations of *A. nodosum*.

Although zygotes dispersed further than expected, long-distance transport (≥100 m) of zygotes among shores seems unlikely. Long-distance dispersal of algal spores appears to be episodic and associated with storms (Reed, Laur & Ebeling 1988), and the reproductive behaviour of *A. nodosum* may preclude even episodic long-distance transport of zygotes. The range of zygote dispersal of *A. nodosum* is probably consistent with the estimated maximum range of 30 m previously reported for fucoid algae (Chapman 1995). Long-distance migration of *A. nodosum* probably occurs only via rafting of detached, fertile fronds (e.g.

from ice scour). Given the longevity of individual thalli (Åberg 1992a; Åberg 1992b), such founder events may establish populations.

DOES DISPERSAL LIMIT THE RECRUITMENT OF *A. NODOSUM*?

The recruitment of *A. nodosum* declines exponentially with distance from the edge of an adult stand, and is near zero less than 4 m away (Dudgeon & Petraitis 2001). The hypothesis that limited dispersal caused this pattern affected the design of the present study, the data from which suggest that the recruitment decline of *A. nodosum* with distance from a stand is caused by early post-settlement mortality, rather than limited dispersal. More than 50% of zygotes dispersed beyond 6 m. In contrast, the density of recruited germlings declined approximately 40-fold over a distance of 2 m from the edge of a stand, and declined further beyond 2 m (Dudgeon & Petraitis 2001). This discrepancy is probably attributable to the protective effect of an overlying canopy. At sheltered sites such as these, *A. nodosum* thalli are approximately 1–2 m long, which coincides with the range of recruitment.

The implication of post-settlement mortality (Viejo *et al.* 1999) – rather than dispersal potential – as the cause of the recruitment patterns of *A. nodosum* suggests that the germling stage (0–1 years of age) is critical to the demography of the species. Like most marine species with external fertilization, *A. nodosum* is believed to exhibit a type III or IV survivorship curve at the extremes of its distribution on moderately exposed shores (Vadas *et al.* 1990). But unlike many species with similar survivorship curves, newly recruited germlings of *A. nodosum* are uncommon. The population structure consists primarily of adults that allocate approximately 50% of their biomass to gamete production annually (Åberg & Pavia 1997). This pattern of adult domination of populations occurs even on sheltered shores. Perhaps the key to understanding the population dynamics of the most abundant intertidal organism in the North Atlantic Ocean lies in a demographic analysis of its first year of life.

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