

Analysis of Environmental Gradients and Patchiness in the Distribution of the Epiphytic Marine Hydroid *Clava squamata*

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ABSTRACT: Distributions of the hydroid *Clava squamata* and the alga *Ascophyllum nodosum* were examined in relation to two major environmental gradients: a gradient of wave action extending from a sheltered bay to an exposed point, and the vertical gradient produced by tidal exposure. These gradients were obvious in the distribution of sediment types, but measurements of abrasion using pieces of chalk were only correlated with the duration of immersion. A preliminary survey based on one metre square quadrats revealed a marked patchiness in the distributions of both, hydroid and alga. Two horizontal line transects, of 1,160 m total length, provided striking illustrations of the patchy distribution of the hydroid. There was a significant decrease in the density of *C. squamata* colonies on the higher of the line transects (mid level) compared with the other transect (low level) only 70 cm below it. The growth form of *A. nodosum* varied over both the horizontal and vertical gradients on the shore, and *C. squamata* preferred sheltered sites for settling on the plants. Centres of maximum density of hydroid colonies were recognizable in several plants suggesting, along with the marked patchiness in overall distribution, that *C. squamata* is distributed by benthic (crawling) larvae. Adult hydroid colonies withstood osmotic stresses of half, and double the normal salinity, in laboratory experiments.

INTRODUCTION

Clava squamata (Müller) is a naked colonial hydroid found only upon the algae *Ascophyllum nodosum* (L.) and *Fucus vesiculosus* (L.). This animal is locally abundant in regions of dense *A. nodosum* growth where there is shelter from waves (Williams, 1965) and is unusually dense at Granagh Bay, Strangford Lough, Co. Down, N. Ireland, where the colonies of *C. squamata* have persisted for many years.

Granagh Bay is several miles inside the mouth of Strangford Lough and is sheltered from all sea waves except those from the SE, but even these are largely barred by a series of sunken rocks and small islands (Fig. 1). There is a very strong tidal current past the bay, four knots and over, but a slower current flows through it. *Ascophyllum nodosum* is very abundant within the sheltered area, but decreases markedly in the open narrows north of Rue Point. *Clava squamata* is extraordinarily abundant within the sheltered area, over 400 colonies have been found on one plant. This

area seemed ideal for studying gradients in the distribution of *C. squamata*, both horizontal from sheltered to exposed regions, and vertical within the intertidal range of the plant. The present study was based upon factors that could be measured without specialized apparatus, and within the restricted time available (early March, 1979).

MATERIALS AND METHODS

Quadrat Survey

A pilot survey of *Clava squamata* colonies on *Ascophyllum nodosum* was performed in an area 20 m by 44 m using 22 traverses of 2 m width. The number of colonies was recorded separately for each square metre. This area included the entire vertical (intertidal) range of the plant in this shore region (Fig. 1).

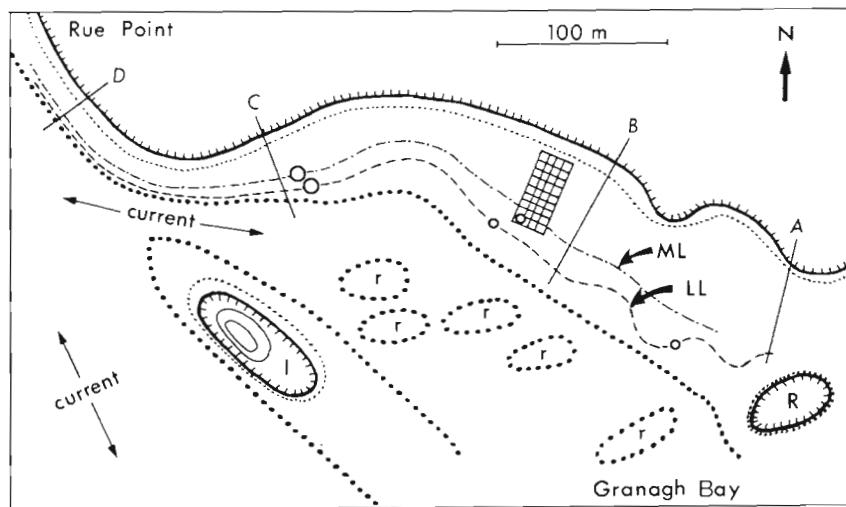


Fig. 1. Map of area studied: Granagh Bay, Strangford Lough, North Ireland. Distribution of *Ascophyllum nodosum*: lower limit, large dotted lines; upper limit, small dotted lines. Shelter from waves provided by island (I), exposed rock (R), and tide-covered rocks (r). Analyses were: quadrats (grid), lower level line transect (LL), mid-level line transect (ML), vertical line transects (A,B,C,D). Major patches of *Clava squamata* shown by circles. (Prepared from a compass survey)

Horizontal Line Transects

Two line transects were made, each of sufficient length to reach from the sheltered bay area in the east to the exposed point in the west (Fig. 1). The lower level transect was made at the lowest level of *Ascophyllum nodosum* by following the waterline at low tide for a distance of 620 m. In effect, the tide drew a contour line for us. The mid level transect was set by eye 70 cm above the level of the lower transect, and thus 3–7 m further up the intertidal zone. Because of fewer irregularities in the contour at this elevation, the mid-level transect was only 540 m long. The transects were made using two survey parties, each recording the number and location (to the nearest 10 cm) of colonies of *Clava squamata* found within 20 cm of the rope. All colonies were counted up to 20, but larger groups were estimated. The two transect ropes were laid end to end but the parties worked at different speeds and 'leapfrogged' one another in consecutive 20 m blocks. Thus with two survey parties, the 'leapfrogging', and the natural 'contour lines', we believe that any systematic sampling bias was destroyed.

Density of Colonies

During the line transects, single individuals of *Ascophyllum nodosum* were periodically collected and taken to the laboratory for analyses of wet weight, maximum length, number of bladders, and number and location (to the nearest 1 cm) of colonies of *Clava squamata*.

Growth Form of *Ascophyllum nodosum*

Length and Weight

A separate set of four vertical transects was made to examine the length and weight of the plant (see Fig. 1). At each transect four stations were spaced evenly: No. 1 at the highest level of *Ascophyllum nodosum* growth, No. 4 at the lowest level of this growth (equivalent to the lower level line transect); Nos 2 and 3 were intermediate. At each station 2 (rarely 3) plants were weighed and the maximum length recorded. The 34 measurements of each factor were analyzed for normality (Cassie, 1950, 1954) and were each characterized by a major normal distribution, so the data were used without transformations.

'Bushiness'

Ascophyllum nodosum tends to branch a short distance above each bladder, especially in the upper ends of the fronds. Tall plants, and especially older ones, tend to have a main stem with 'extra' bladders, that is bladders without branches above them, although some older plants branch repeatedly from the same levels of the main stem. Large plants also tend to lose side branches. These different tendencies interact to produce a great variation in form of plants found in the area studied, reaching the extremes of a 25-fold difference in weight for plants of the same length. This variability negated comparisons of weights in the horizontal direction (Table 2). A more sensitive basis was

sought for detecting environmental influences on the plant.

The length of the longest frond and the number of bladders on it were plotted for every plant collected. The average distance between bladders was 15.5 cm for virtually all plants studied. With this stable spacing, and branching above the bladders, plant weight should increase as a simple multiple of length and a semi-logarithmic plot described the relationship. This plot was used to estimate the median weight for a plant of a given length, and actual weight divided by median weight gave a value for 'bushiness'. These 'bushiness' values were then analyzed for environmental influences.

Sediment Types

Samples of the sediment were collected at each of the 16 stations of the vertical transects and the appearance of the shore was recorded. Portions of the collected material were shaken with sea water, allowed to settle overnight, and the qualitative appearance used to augment the field observations.

Abrasion

The relative exposure to waves and currents at several sites was measured using small pieces of soft blackboard chalks. We cut, drilled out the centre, and trimmed these pieces so that a random sample of 20 weighed a total of 26 g. These pieces were smaller and lighter than the gypsum balls used for estimating exposure by Muus (1968) and Boaden et al. (1975). A single individual of *Ascophyllum nodosum* was chosen at each test site and 20 weighed pieces of chalk tied on individually so as to prevent their rubbing together. The chalk was left in place long enough to undergo two periods of tidal immersion. A control of 20 pieces was kept in the laboratory in sea water for the same length of time. Abrasion was estimated from the reduction in weight of the exposed pieces.

Settling on Specific Sites on *Ascophyllum nodosum*

Five very densely colonized plants from the region of the largest patch on the low level transect were examined and the occurrence of *Clava squamata* on 4 specified sites was recorded. A total of 1000 colonies was counted. The four sites on *Ascophyllum nodosum* were:

- (1) The mid regions of bladders (a in Fig. 5), the most exposed region.

- (2) Branching points or forks (b in Fig. 5), the most sheltered region.
- (3) Junctions of bladders and stems (c in Fig. 5), a partially sheltered region.
- (4) Mid regions of stems (d in Fig. 5), exposed, but less so than the bladders.

Estimating the Frequency of Sites

Because of the irregular growth of this plant, a theoretical basis was sought for derivations of the frequency of each site. These frequencies were based upon a series of plans for branching (Fig. 5) which were expanded and formed convergent series of values as the number of branches increased. The plans for branching themselves are part of an overall series with two ultimate sets of frequencies: In the extreme case of a plant with no side branches the frequencies are: a, 25 %; b, 0 %; c, 50 %; d, 25 %. In the equally unlikely case of a plant without bladders, but with many side branches these frequencies are: a, 0 %; b, 50 %; c, 0 %; d, 50 %. Plants collected had on average, one or two side branches above each bladder, roughly midway between the two calculated extremes.

Osmotic Stress

Since *Ascophyllum nodosum* is an intertidal plant, *Clava squamata* must occasionally be exposed to rain or sun, thus the salinity of the surrounding water film would be increased or decreased. The duration of such exposure would depend upon height on the shore. Resistance to osmotic stress was measured in the laboratory using 5 separate colonies in each experiment. Normal sea water (at Portaferry) was either diluted or had salt added as required. All colonies were observed to be normal before use, retracting their tentacles when touched. They were then placed in the prepared medium and observed after 3 h, and again after 10–13 h. The test medium was then replaced with normal sea water and the colonies checked for recovery after 3 h. A control was used and the tests were made at the ambient sea temperature of 8.5 °C.

RESULTS

Quadrat Survey

The patchy distributions of both plant and hydroid are obvious (Fig. 2). *Clava squamata* is more unevenly distributed than the alga with the densest patches of

hydroids at the lowest level. The highest level, even with abundant alga, had no hydroids. The growth form of *Ascophyllum nodosum* varied greatly over this vertical range, from tall plants with numerous bladders on the lower shore, to short plants with numerous conceptacles on the upper shore. There was a corresponding change from boulders on the lower shore to black mud on the upper shore.

Line Transects

Four trends are apparent in the distribution of *Clava squamata* (Fig. 3):

- (1) There is a marked patchiness with distances of approximately 200 m between the three largest patches on the lower level transect.
- (2) Cross sections through the largest patches, as represented by the transects, have the appearance of

graphs of the normal distribution. This is clearer if the bars showing the distribution of *Ascophyllum nodosum* in Figure 3 are covered with a piece of paper.

- (3) There is no large patch towards the exposed region at Rue Point.
- (4) The two largest patches on the mid level transect coincide with those on the lower transect.

This was the pattern obtained by averaging the counts for each linear metre; a finer analysis was made by dividing the individual counts of colonies into 4 increasing patch sizes: 1–4, 5–16, 17–49, 50 and upwards. These groups reveal in a more substantial way the differences between the two levels (Table 1). The lower level has more larger patches than the mid level, but there are similar numbers of smaller patches. Overall, the four patch frequencies were just significantly different ($P < 0.05$, $\chi^2 = 7.91$). The total counts of colonies were: lower level, 2099; mid level, 1273.

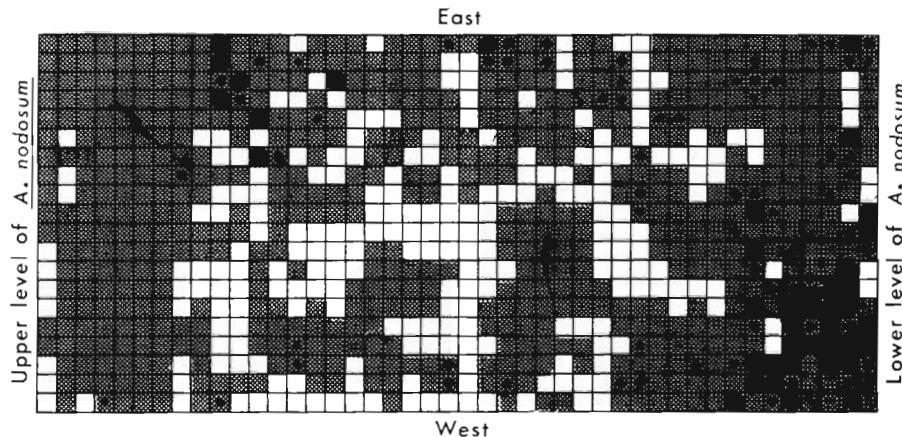


Fig. 2. Quadrat survey on 1 square metre grid. Areas without *Ascophyllum nodosum* unshaded. Density of *Clava squamata* colonies in each quadrat: small dots = 1–4; large dots = 5–16; octagons = 17–64; solid squares = 65 and over

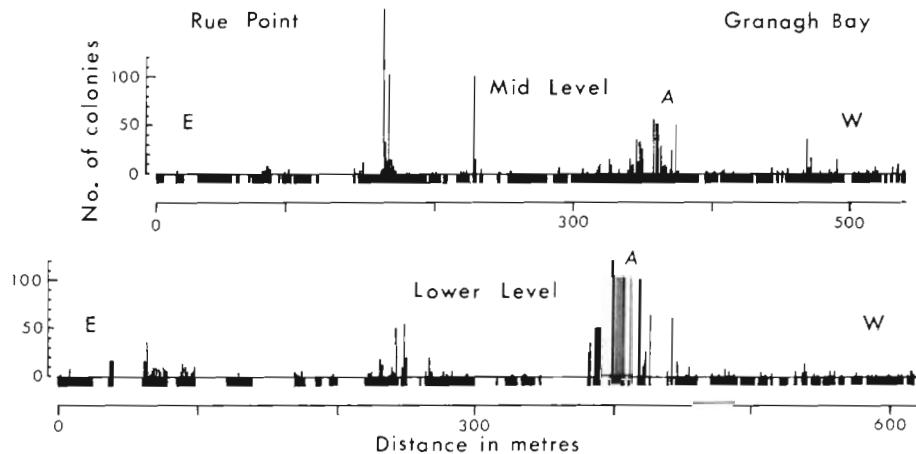


Fig. 3. *Clava squamata*. Horizontal line transects showing patchiness, and the number of colonies in each metre. Unshaded areas below baseline mark regions without *Ascophyllum nodosum*. Both transects were begun at the east (E) but coincide in cross section only towards the west (W). The two patches (A) are one very large patch on the shore

Density of Colonies

The density of *Clava squamata* colonies on plants (plants without hydroids not included) was significantly lower at the mid level (95 % C. L. 5.6–15.8, n = 7) than at the lower level (10.6–45.0, n = 9) ($P < 0.05$, $t = 2.15$). There were also more uncolonized plants at the mid level (6/13) than at the low level (1/10). There were no differences in weights and lengths of plants to correspond with the difference in colonization (95 % C.L., mid level wt, 196–542 g, ht 119–165 cm, n = 7; low level wt 228–544 g, ht 105–163 cm, n = 9).

Growth Form of *Ascophyllum nodosum*

Length and Weight

The average measurements of length and weight taken at the 4 vertical transects (16 stations) showed a decrease in both factors as height on the shore increased. These averages were inconsistently affected by the transition from sheltered to exposed parts of the shore. Two-way analyses of variance (ANOVA) showed that variations in length were significant for both vertical and horizontal position on the shore, but plant weight was so variable that only vertical position (shore level) approached having a significant effect (Table 2A, B). Despite the general patchiness there

Table 1. *Clava squamata*. Patches of colonies found on the horizontal line transects

Patch size (numbers)	Transect	
	Lower level	Mid level
50	17	7
17–49	8	3
5–16	44	42
1–4	92	109
Total colonies counted	2099	1273

were no interaction effects. Since proof of consistent directional trends was wanted, correlation coefficients (r) were computed. These showed that plant length was very highly significantly affected by shore level (decreasing from lower to upper shore), but no other correlations were significant (Table 2D).

'Bushiness'

The average values pointed to a general decrease in 'bushiness' as the exposed region was approached, but there was an inconsistent effect of level on the shore. A two-way ANOVA confirmed that horizontal position had a highly significant effect, but that vertical position was insignificant (Table 2C). The correlation coefficient showed a highly significant and therefore consistent trend towards a decrease in 'bushiness' as the exposed Rue Point was approached (Table 2D).

Table 2. *Ascophyllum nodosum*. Growth form related to environmental gradients

Source	(A) ANOVA of weight			F	Significance
	Degrees of freedom	Mean square			
Level on shore	3	784,419		2.88	0.075
Horizontal position on shore	3	62,741		0.23	NS
Interactions	9	359,723		1.32	NS
Deviations	16	271,465			
	(B) ANOVA of length				
Level on shore	3	9,832		11.7	0.005
Horizontal position	3	2,701		3.2	0.05
Interactions	9	1,049		1.2	NS
Deviations	16	841			
	(C) ANOVA of 'bushiness'				
Level on shore	3	20,052		1.68	NS
Horizontal position	3	72,409		6.05	0.01
Interactions	9	19,126		1.60	NS
Deviations	16	11,952			
	(D) Correlation coefficients				
Factors	<i>r</i>	Significance (33 d. f.)			
Weight/Level on shore	0.154	NS			
Length/Level on shore	0.705	0.001			
'Bushiness'/Level on shore	0.034	NS			
Weight/Horizontal position	0.112	NS			
Length/Horizontal position	0.255	NS			
'Bushiness'/Horizontal position	0.499	0.01			

Table 3. Sediment types at the stations of vertical transects

Level	Rue Point (Exposed)			Granagh Bay (Sheltered)	
	D	C	Transect	B	A
1	Pebbles, some sand and silt	Gravel and rocks		Black silty sand	Black silty sand
2	Small gravel	Coarse sand with some silt		Grey silty sand	Black silty sand
3	Coarse gravel and boulders	Small pebbles and silt		Grey silty sand, some pebbles	Black silty sand
4	Coarse gravel and boulders	Grey silty sand and broken shell		Grey silty sand	Grey silty sand

Sediment Types

The results (Table 3) are laid out showing Transect A to the east, as in Figure 1. There was a general trend from finer sediments on the upper shore, to coarser ones at the lower limit of *Ascophyllum nodosum* growth. In the horizontal direction, there were finer sediments overall in the sheltered sites at Transect A, and coarser ones towards the exposed Rue Point. There are two complimentary gradients here and a diagonal line from Station A1 to Station D4 has the greatest

range of sediments, from fine anaerobic silt at the highest sheltered point, to coarse gravel and boulders at the lowest, most exposed point. This range of sediments gave the clearest indication of a gradation in environmental conditions over the area studied.

Abrasion

For the first trial, 20 pieces of chalk were placed at the lower level transect at Rue Point, and the same again in the region of the largest patches of *Clava squamata* (Fig. 1). A gale force N wind overnight produced waves from Strangford Lough and both sets of chalk were abraded severely (74 % wt loss at Rue Point, 77 % wt loss at the sheltered site).

For the second experiment, chalk was placed at low and mid levels at Rue Point, and at low, intermediate, and mid levels near the largest *Clava squamata* patches. This night was calm but spring tides with strong currents operated. Abrasion was severe at the low level of the sheltered site (84 % wt loss) and only moderate at the low level at Rue Point (57 % wt loss). The mid level chalk lost 23 % of its weight at the sheltered site, but 30 % at the exposed one. The intermediate chalk (sheltered site) lost 75 % of its weight. The most important differences here appeared to be the very great weight loss at the low level sheltered site, and the consistently greater losses at low levels overall.

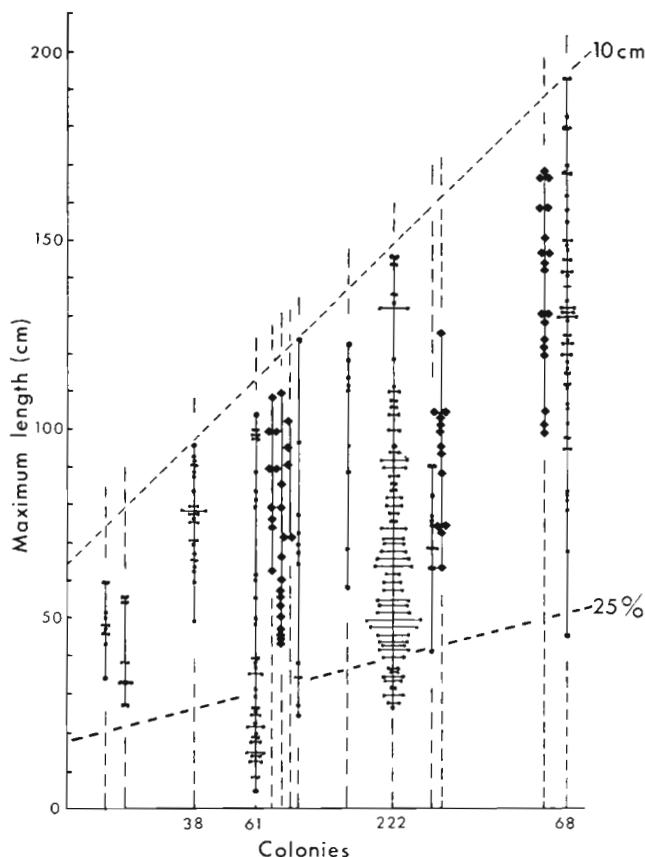


Fig. 4. *Clava squamata*. Vertical distribution of colonies on individual *Ascophyllum nodosum*. Total no. of colonies given where not drawn on the figure (e.g., 222). Solid dots: low level transect; squares: mid level transect; regions 10 cm below the tips and 25 % of length above the holdfast are shown

Vertical Distribution of *Clava squamata* on Individual Plants

Because of the considerable numbers of colonies on 5 of the 9 plants from the lower level transect, regions of maximum concentration could be plotted. These were virtually in the centre of their vertical distribution on three plants, while two others had colonies concentrated towards the base (Fig. 4). There was an average of 28 colonies per plant, extending over 44 % of the plant length. The 5 plants from the mid-level transect carried an average of only 11 colonies, extending over

30 % of total plant length. The hydroids were therefore nearer both the tips and the bases of the low-level plants (Fig. 4).

Settling on Specific Sites on *Ascophyllum nodosum*

The distribution of the 1000 colonies was compared with the extremes of the calculated branching series,

and with the 2 observed plants. The values are very highly significant in all cases (Table 4). It is quite clear that *Clava squamata* prefers the sheltered site of the forks, reducing the colonization of other sites. The very exposed, bulbous surfaces of the bladders were least acceptable as a settling site, colonies found there had developed around pits in this otherwise unprotected region of the plant.

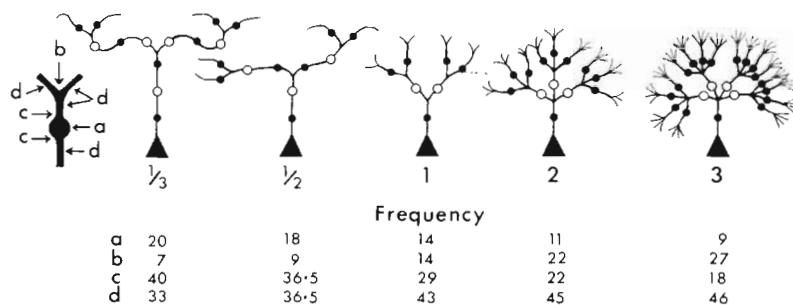


Fig. 5. *Ascophyllum nodosum*. Possible growth forms including the following: 1 side branch per 3 bladders ($\frac{1}{3}$), 1 branch for 2 bladders ($\frac{1}{2}$), 1 branch per bladder (1 = a dichotomous plan), 2 branches per bladder (2 = a trichotomous plan), 3 branches per bladder (3). Frequencies of the following 4 sites are given beneath each diagram: (a) mid regions of bladders, (b) branching points of forks, (c) junctions or bladders and stems, (d) mid regions of stems

Table 4. *Clava squamata*. Observed distribution of 1000 colonies compared with frequencies of sites according with different growth forms

	Bladders (mid regions) (a)	Bladders (junctions) (c)	Forks (b)	Stems (mid regions) (d)	Total
Observed frequency	8	157	671	164	1000
Growth form		Observed/Calculated frequency			χ^2
no branches	8/250	157/500	671/0	164/250	346*
1 branch per bladder	8/140	157/290	671/140	164/430	2363
2 branches per bladder	8/110	157/220	671/220	164/450	1219
no bladders	8/0	157/0	671/500	164/500	284*

* Values for empty cells in extreme cases not counted.

Table 5. *Clava squamata*. Responses to changed salinities. Five colonies were used in each experiment and in each case, all responded similarly

Environment	Condition of colonies	
	Changed salinities, 13 h duration	Returned to normal sea water
Salinity		
Normal (33 ‰)	Normal*	Normal
Fresh water	Bloated, tentacles retracted	Bloated, dead
$\frac{1}{4}$	Bloated, tentacles retracted	Bloated, dead
$\frac{1}{2}$	Tentacles retracted	Normal
$\frac{3}{4}$	Normal	Normal
2	Bodies and tentacles retracted	Normal
Excess**	Bodies and tentacles retracted	Bloated, dead

* Normal colonies retracted their tentacles when touched. All such colonies were alive after 24 h.
** Salt crystals lay on the bottom of the vessel.

Osmotic Stress

Clava squamata recovered from dilutions as low as $\frac{1}{2}$ normal salinity (normal salinity = 33 ‰), but below this the colonies became bloated during the experiment and did not recover (Table 5). The colonies also recovered from double the normal salinity, but not from a saturated salt solution where the polyps lay on the crystals. In every test all 5 colonies behaved alike, although they varied in the speed of their initial response to the test medium.

DISCUSSION AND CONCLUSIONS

The patchiness in both plants and hydroid revealed by the quadrat survey led us to use the quicker and more extensive line transects. Here the patchy distribution of *Clava squamata* was even more obvious. Modern computational methods are now applied to prove clumping (e.g., Clark and Evans, 1954; Waloff and Blackith, 1962), but Figures 2 and 3 are self evident. Since there are isolated patches of colonies (Table 1) some larvae must be transported by currents to settle new areas. This may be the condition under which environmental gradients act most strongly.

Once an initial colony is established, the subsequent development of a large patch of colonies could be the result of restricted movement of the larvae. Planulae of *Clava squamata* have been observed to crawl immediately upon being released by the parent (Williams, 1965). These larvae could easily transfer between adjacent plants at low tide when the plants are heaped together. New generations of crawling larvae could gradually extend the patch. If on the other hand, the larvae were spread in the plankton, even a current as slow as one knot would move them 200 m in only $6\frac{1}{2}$ min – the distance between the largest patches found here. Since unattached larvae have been found to live for up to 30 h in the laboratory (Williams, 1965) a planktonic mode could lead to a wide and even distribution over the relatively uniform *Ascophyllum nodosum* beds in Granagh Bay. The very patchy distribution of *Clava squamata* argues for the crawling mode of dispersal.

Centres of density on individual plants also argue for dispersal by crawling. These centres could be produced by randomly filling the preferred sites nearest the original colony, with only a small proportion of larvae moving further away. The extension of vertical range on individual plants would occur as successive generations of larvae searched over greater distances before finding their preferred settling sites. The extension of vertical range on individual plants as density increases appears to be another case of increasing niche breadth

with greater intraspecific competition, as found by O'Connor et al. (1975) for the ectoproct *Alcyonium hirsutum* colonizing *Fucus serratus*.

Because of the patchiness a clear gradient in the horizontal distribution of the hydroid was not apparent. However, there were no large patches near Rue Point (field observations) and there is no indication of a buildup to them from the histograms (Fig. 3).

The best indication of a vertical (intertidal) environmental gradient in *Clava squamata* was the reduced density of colonization on mid-level transect plants compared with low level plants. The 4 vertical transects revealed real differences in weight and length of *Ascophyllum nodosum* over its vertical range, confirming what can be sensed in the field, there is a marked decrease in the size of plants towards the upper limit of their range but a horizontal trend from sheltered to exposed regions of the shore is difficult to perceive.

The 'bushiness' values were sensitive to a horizontal gradient in some environmental factor, possibly to a tendency for bulky plants or portions of them to be torn loose in storm. Thus small plants were found at all levels of the shore at Rue Point and very large plants with many branches were found in the sheltered region of the largest patches. The three indices weight, length and 'bushiness' may respond to different stresses, with exposure time or depth of immersion affecting the first two (Table 2).

A horizontal gradient in sediments clearly extended from sheltered to exposed regions and corresponded with the gradient in 'bushiness'. Boaden et al. (1975) analyzed a similar relationship between the 'branching index' in *Fucus serratus* and variations between sampling sites distributed over a gradient of distance from the mouth of a shallow basin. Their results were not significant, but their sites were all well sheltered from waves.

Our few measurements of abrasion show a reduction in this factor as height on the shore increased. It appears that currents are more important than waves here, since the greatest abrasion occurred during calm weather at spring tide. Since the mid-level chalk was immersed for the shortest times it would be abraded least by currents. Stronger currents at lower depths, plus longer time of immersion, would cause the low-level chalk to be severely abraded. Boaden et al. (1975) found that abrasion was positively correlated with the abundance of *Fucus serratus* and our results are similar. There are larger plants at low levels where the currents are stronger, or where the plants are exposed to currents for longer periods. We have only found that these two factors coexist and do not expect that abrasion promotes growth, but that longer immersion, greater depth of water and less drying and freezing are all conducive to larger plants.

Abrasions obviously had no detrimental effect upon adult *Clava squamata* since the greatest abundance of colonies was at the lowest, most abraded level. Again, this may imply that longer immersion allows longer feeding time and less overall environmental stress. There is a flourishing tunicate fauna at Grangh Bay as well, probably due to the abundance of current-borne food. Boaden et al. (1975) found a positive correlation between abrasion and the abundance of several sessile animal species on *Fucus serratus*. Abrasion as estimated in our study might then be looked upon as a chronic (sublethal) but not a critical factor for adult *C. squamata*.

Whatever the form of this very variable plant, there is no loss of significance in the distribution of the colonies of *Clava squamata*. Crevices are preferred for settling sites, perhaps because of the abrasion just referred to. These findings in distribution agree with those of Williams (1965), but he did not examine the frequencies of the sites themselves. A future step in this analysis will be to examine patterns in the distribution of colonies on individual plants, especially in conjunction with their density.

Although the polyps of each colony must trap sea water between them when they are exposed by the tide, and so have some buffer against the ambient climate, they are surely better protected in the middle of the plants than at the extremities. Even in March a coating of salt appeared on the plants during one gale-swept afternoon. *Clava squamata* did not withstand such an extreme in the laboratory and this may account for its absence from the highest part of the fronds. The resistance of this hydroid to osmotic stress is still striking, especially since the laboratory tests were carried out for longer than the normal exposure time between tides.

This work points to the existence of gradients in all the directions studied, horizontal and vertical on the

shore, and vertical on the plants. Of course these gradients have only been deduced from their effects upon *Ascophyllum nodosum*, the composition of the sediment, and the distribution of *Clava squamata*. What the effective factors are, whether they are abiotic or biotic, and whether they are similar or not for the plant and the hydroid are questions requiring much future work.

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