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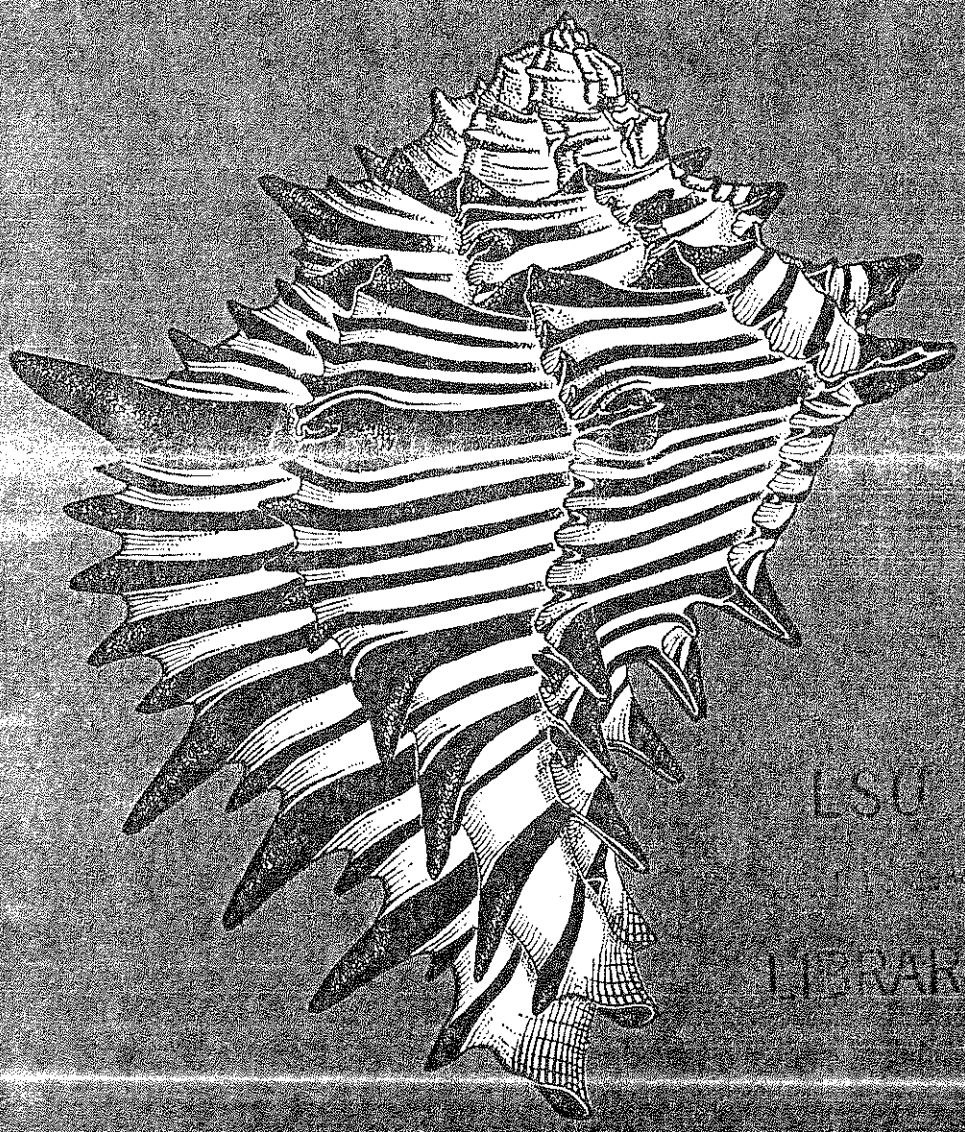

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REDISTRIBUTION AND LOCAL RECOLONISATION BY THE FRESHWATER PEARL MUSSEL *MARGARITIFERA MARGARITIFERA* (L.)

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(*Accepted for publication 19 March 1983*)

Abstract: *M. margaritifera* is shown here to be a largely sedentary animal, which can move short distances, however, if its habitat changes. It requires a stable substrate of coarse sand, where it burrows to varying depths, and it does not occur in streams where the substrate is substantially resorted by torrents. In these it fails to establish and is washed away. Recolonisation of denuded areas can only be achieved very slowly by adult mussels and the main source of colonists is certainly young mussels being released from host fish. When large mussels suddenly reappear in denuded areas it is probable that these are specimens which were previously completely buried and have since burrowed up into view.

INTRODUCTION

The freshwater pearl mussel, although usually regarded as a sedentary animal, has the ability to burrow and to move about slowly and rather inefficiently (Davis and Fuller 1981). The mechanism by which this is achieved is described by Trueman (1968). However there is no agreement about whether the mussels do ever move significant distances naturally (although Boycott and Bowers (1898) assert that they do) and this is generally discussed with reference to two main problems. First of all whether young mussels occupy a different substrate type to older mussels, moving between these substrates as they grow; and secondly whether mussels can redistribute themselves and recolonise areas which have become vacant, either through natural displacement or through man's pearl fishing activities, (Jackson 1925, McCormick *pers. comm.*). This study aims to provide evidence to answer these questions.

A population of the freshwater pearl mussel was studied in the Stac Burn, Iverpolly N.N.R., Wester Ross from 1978 to 1981. Here two areas were artificially denuded of mussels and recolonisation was monitored; the mussels in two other areas were mapped precisely each month so as to observe natural movements; and marked mussels were moved to a tributary stream which was torrential and naturally devoid of mussels, so as to observe whether mussels moved more there than in the Stac Burn. It was hoped to distinguish between voluntary and involuntary movements of mussels by close comparison between their movements and those of similarly sized stones.

STUDY AREA AND METHODS

The Stac Burn, Inverpolly N.N.R., Wester Ross (NC 0812) is a typical Scottish west-coast mussel habitat. It has an abundant mussel population, which has apparently been fished only occasionally, and is small enough to be accessible even in winter high-water

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TABLE 1

Movement of mussels into two areas artificially denuded of them in the Stac Burn, Inverpolly N.N.R., Wester Ross.

		Date of observations[1]																					
	Sept 1978	10	12	2/79	3	4	5	6	7	8	9	10	11	1/80	2	3	5	6	8	9	11	3/81
Area 1																						
Total No. found in area	0	0	2	1	1	4	5	5	6	8	7	8	7	7	7	8	8	9	9	10	12	10[2]
No. found in 0.50 m edge of area	0	0	1	1	1	2	2	2	2	3	3	3	3	3	3	3	3	4	4	5	6	5
Area 2																						
Total No. found in area	0	6	4	5	4	7	8	8	10	9	10	11	11	11	9	10	10	11	11	10	10	12[2]
No. found in 0.50 m edge of area	0	4	2	3	3	4	4	4	5	5	5	6	6	6	4[3]	5	5	6	6	6	6	8

1) Note: time intervals are not equal.
2) Includes central group of up to 6 small, buried mussels, difficult to locate and immobile.
3) 2 marginal mussels moved out of area.

Area 1—1·5 m × 2 m, Area 2—2 m × 3 m. Both denuded of mussels in September 1978

levels. It is approximately 3 m wide, generally 0·20–0·50 m deep and flows from a small loch to join the River Polly. Its substrate is a variable mixture of course sand, gravel, stones and some boulders, and mussels are found throughout it except in one or two very small sandy areas. Its substrate composition, and that of its main tributary, was assessed subjectively according to a modified Wentworth classification (Wentworth 1922).

1. *Recolonisation experiments*

Two areas, which were easily delimited by reference to emergent marker stones, and which contained mussels at a representative density for the Stac Burn, were denuded of all mussels as far as possible. In the immediately surrounding areas normal mussel populations remained and there was no barrier of any sort between these populations and the denuded areas.

The denuded areas were observed at intervals for 30 months from September 1978 and all mussels within them mapped to the nearest 30 mm. One of these areas was approximately 1·5 m × 2 m (area 1 of Table 1) and the other 2 m × 3 m (area 2 of Table 1).

2. *Observations of natural mussel movements*

In October 1978 two areas were chosen, one 1·5 m × 2·5 m (area 1 of Table 2) and one 2 m × 2·5 m (area 2 of Table 2), each of which contained a representative density of mussels (about 65–70 each). These mussels were moved so that the mussels were approximately evenly distributed throughout the areas and were then left to re-establish themselves. The mussels in one area were mapped from October 1978 to March 1981 and in the other from August 1979 to November 1980. In each case mussels were located at least to the nearest 30 mm and could usually be located more precisely by reference to the position of stones.

3. *Mussel loss from a torrential stream*

In September 1979, 20 mussels were marked using a technique described by Young and Williams (1983) which does not harm the mussels. These were then placed in apparently suitable areas 30 m up a tributary of the Stac Burn. The tributary is similar to the Stac Burn

TABLE 2.

Movement of mussels within two mapped areas of the Stac Burn, Inverpolly, N.N.R., Wester Ross.

		Date of observations[1]																						
	Oct 78	12	2/79	3	4	5	6	7	8	9	10	11	1/80	2	3	5	6	8	9	11	3/81	No's and % unmoved
Area 1																						
No's in area	65	58	56	58	62	66	70	74	75	74	76	75	74	72	74	76	75	73	68	69	68	11/79 to 11/80
No's moved in interval	—	10	8	12	4	5	7	10	6	4	4	3	2	2	2	5	8	14	13	9	2	18
% moved in interval	—	17	14	21	6	8	10	14	8	5	5	4	3	3	3	7	11	19	19	13	3	= 26%
Max[m] distance moved—cms	—	20	20	15	15	10	15	25	20	10	20	5	5	5	5	10	20	25	20	15	5	
Area 2																						11/79 to 11/80
No's in area								71	71	70	68	66	66	67	70	69	66	65	64			20
No's moved in preceding interval								3	2	2	6	1	0	2	1	1	8	8	0			
% moved								4	3	3	9	2	0	3	1	1	12	12	0			= 31%
Max[m] distance moved—cms								10	15	10	20	10	—	15	15	25[2]	20	20	—			
Low water				L	L	L	L			L			L	L	L	L						

1) Note: time intervals not equal
2) track clearly visible

Area 1—1·5 m × 2·5 m, Area 2—2 m × 2·5 m. Mussels in both areas distributed and mapped in October 1978

Maximum distance moved=25 cms
Maximum proportion moving=21% (Area 1, March 1979) or 19% (Area 1, August & September 1980)
Average proportion moving=8%

in most respects, except that there is no loch in its catchment area and so it is subject to swift rises in water level, leading to more torrential conditions. At intervals for 14 months these marked mussels were searched for and mapped. No mussels occur naturally in this tributary. A further batch of 20 was similarly introduced and subsequently observed in March 1980.

RESULTS

Recolonisation experiments

The results of the recolonisation experiments, that is the number of mussels found in each of the two denuded areas, is shown in Table 1. It should be noted that in each case some mussels appeared suddenly more than 0·50 m from the edge of the areas. This is a greater distance than any mussels were shown to move in similar time intervals in the 2nd experiments (see below) and these mussels were often seen to be almost wholly buried. It is thought therefore that they survived the denudation and only became apparent when they burrowed less deeply.

Consequently a more realistic figure for the number of invading mussels is shown by the number found within 0·50 m of the area's edge. In some cases the maps show in detail the slow progress of these mussels into the edge of the area, but in no case did such a mussel progress beyond this edge zone. One was found first unburied on the substrate and only subsequently became buried at that site, it seems likely it was washed in from upstream.

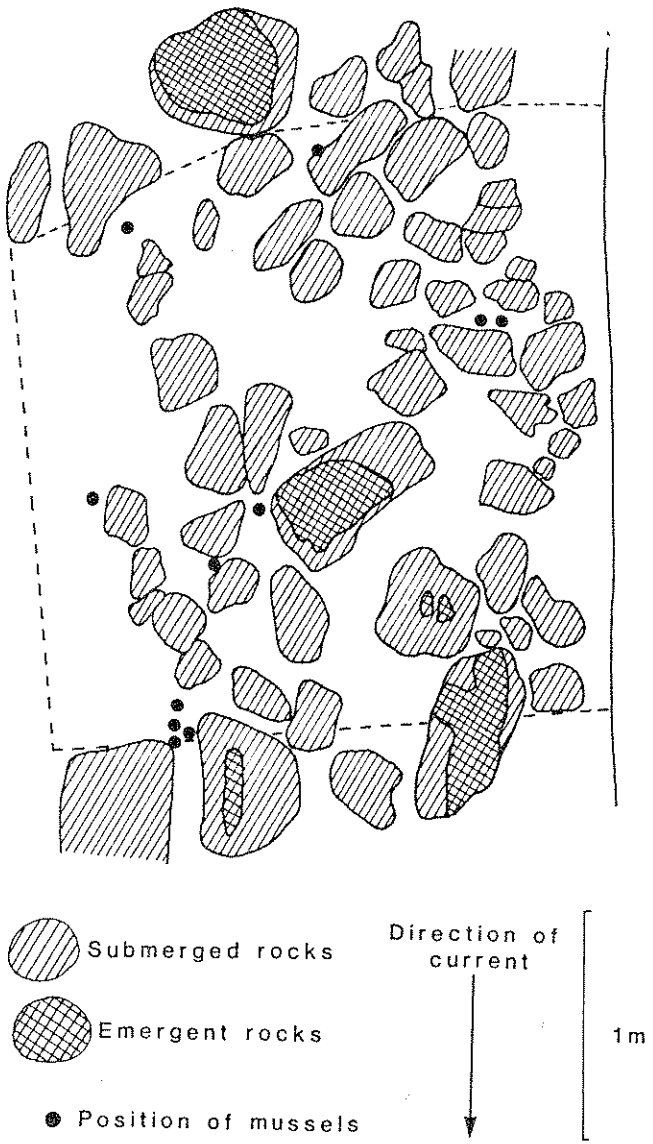

Fig. 1. Recolonisation area 2. The position of mussels in March 1981.

From Table 1 it can be seen that 5 and 8 mussels respectively invaded the edge of the denuded areas in 30 months. (The original number of mussels found in the whole of these areas was about 50 and 70 mussels respectively). Such invasion would only be possible where sand patches are continuous between adjacent areas except for rare occasions when mussels are washed in.

Although the number of invading mussels was too low to allow statistical analysis there was no indication that the invasion was occurring predominantly from any particular direction. Fig. 1 shows the position of the mussels in Area 2 at the completion of the observations in March 1981.

The results show that not all mussels were found each month and this occurred because of the variable depth at which mussels buried and the variable viewing conditions. High, turbid water and overcast conditions sometimes made searching difficult.

Observations of natural mussel movement

Table 2 shows the number of mussels found in each mapped area and the number definitely observed to have moved between each time interval. It also lists the maximum distance moved and the number remaining completely stationary between November 1979 and November 1980.

The fluctuation in total numbers found within the areas illustrates the difficulty of finding mussels, which often bury deeply, under varying stream conditions. It certainly does not represent movement of mussels in and out of the areas.

In both areas the mussels were moved to an approximately even distribution at the start of the experiment. Consequently the initial movements may have been resettling; however, this phase (if it existed) was obviously completed by April/May 1979 when the proportions moving were very low. Although Area 2 was established in October 1978 it was not mapped adequately until August 1979 and so the observations made up till then have been discarded. To avoid both these complications the estimates of numbers remaining immobile were made from November 1979 to November 1980.

The proportion of mussels moving each month varies from 0 to 21% of those present and, up to 31% remained unmoved over a period of one year. In most cases movement is of 50 mm or less but some mussels moved up to 0·25 m in one month. (Laboratory observations have shown that mussels can move 25 cms in less than 1 day under some conditions).

It is clear that the mussels can redistribute themselves over the areas quite actively, presumably in response to changing conditions. These experiments and other casual observations between May 1978 and May 1981 suggest, however, that some mussels rarely, if ever, move. The detailed maps show that these static specimens seem to be those between or behind rocks.

Observed occurrences of very low water are shown in Table 2 but there seems to be no real relationship between them and times of maximum movement. The suggestions from the table that a peak of movement occurred simultaneously in both areas in August and September 1980 supports the view that movement is governed by some overall environmental variable, but this factor remains unidentified.

Observations showed almost no change in the position of even the small stones over the period of observation. Many spates occurred between October 1978 and March 1981 but the substrate was generally unaffected by them.

Fig. 2 shows the position of mussels in Area 1 at the completion of the observations in March 1981.

Mussel loss from a torrential stream

Table 3 shows observations on the loss of marked mussels from a torrential tributary of the Stac Burn. It is clear that a high proportion of the mussels move or are moved out of the

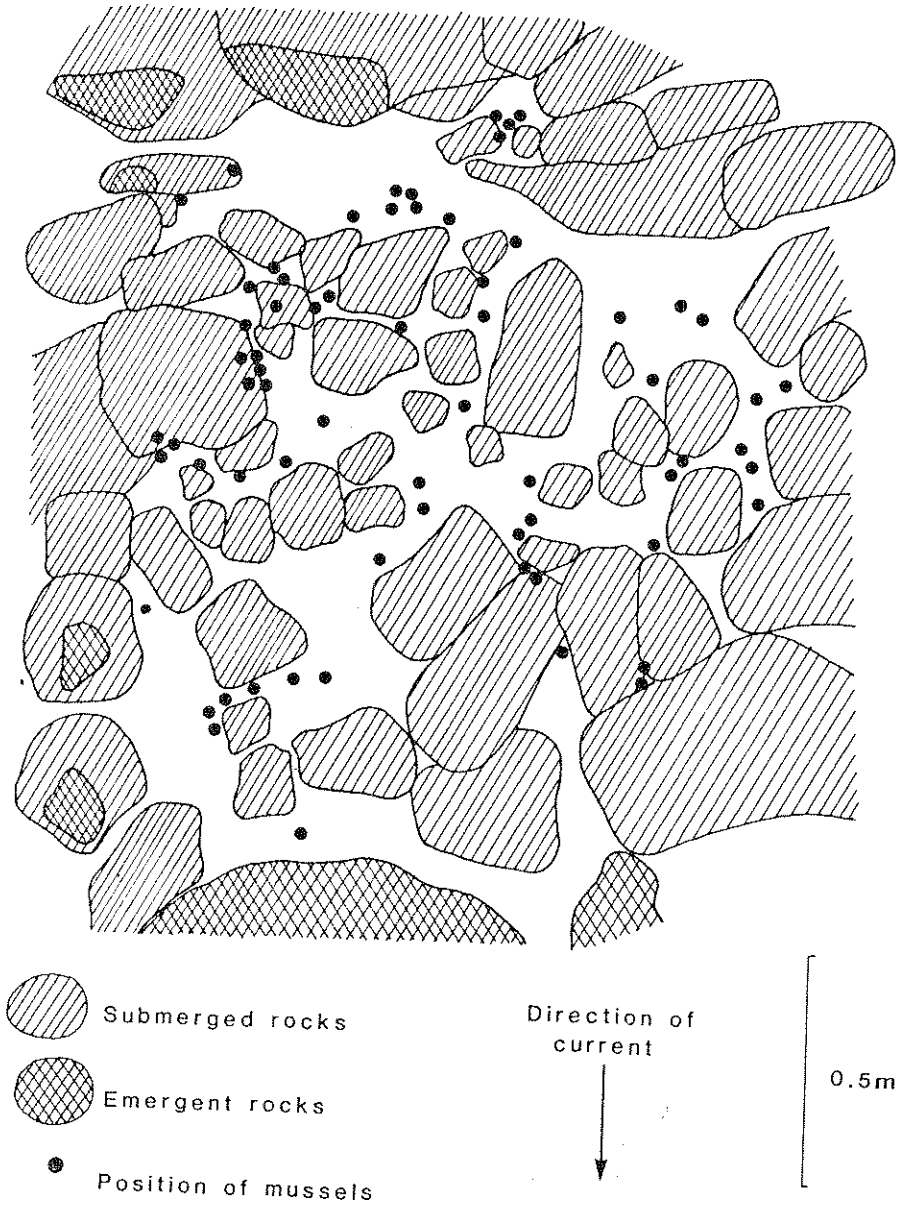

Fig. 2. Mussel movements observation area 1. The position of mussels in March 1981.

TABLE 3

The loss of marked mussels from a tributary of the Stac Burn, Inverpolly, Wester Ross.

	Dates of observations							
	Sept 1979	Oct 1979	Feb 1980	Mar 1980	May 1980	June 1980	Nov 1980	No. & % lost[1]
Batch 1								
No's of mussels present	21	13	11	14	14	11	5[1]	15,=71%
Notes		3 of these found displaced and returned		3 found downstream		1 extra found dead downstream		
Batch 2								
No's of mussels present				20	19	18	9[1]	10,=50%

[1]Two found with missing tags so unattributable to Batch, 1 of these has therefore been attributed to each batch

Losses: Batch 1 71% in 14 months, Batch 2 50% in 8 months

c.f. Maximum possible losses reported in Areas 1 and 2 in Table 2; area 1 11% (8 mussels) in 29 months, area 2 10% (7 mussels) in 15 months.

area of introduction very quickly and some of these were subsequently recovered 10–20 metres downstream. There was a 71% loss from one batch in 14 months and a 50% loss from the other in 8 months. This displacement contrasts so markedly with that noted in Table 2 for the Stac Burn that it seems likely to be a genuine loss due to mussels being washed away.

Areas of coarse sand, such as are frequent in the mussel-inhabited Stac Burn, are much less frequent in the tributary, but there are no significant differences in the water chemistry (Purser *pers. comm*) and Brown Trout are available as glochidial hosts in both. Unfortunately no direct observations were made on the stability of the substrate in the tributary, however subjective assessments were made of the proportion of different substrate types on a modified Wentworth scale. Table 4 lists these proportions and shows the more torrential nature of the tributary by the greater proportion of coarse sediments.

DISCUSSION

It is clear that mussels can move, in suitable substrate, and can recolonise depopulated areas or redistribute themselves after disturbance. It is equally clear that such movement and redistribution is very slow and could not contribute significantly to the recolonisation of a large stream area after its denudation. (Boycott and Bower's (1898) observations that a mussel can move 12–15 feet/day has not been supported by evidence from any later studies). Recolonisation must therefore be achieved by the establishment of young mussels brought to the area as glochidia on their host fish. Only in the torrential tributary were mussels carried passively by the current for any distance, except for 1 specimen noted from Area 2 in the removal experiments.

Adult mussels moving slowly to new areas could obviously not pass rock barriers (except very rarely when being carried passively by the current; it seems inconceivable that they can climb like *Sphaerium* sp.) and in cases where rapid partial replacement of large mussels has

TABLE 4

Subjective assessments of the substrate types of the Stac Burn, Inverpolly, Wester Ross and its main tributary.

Substrate types (modified Wentworth scale)	Stac Burn % composition	Tributary % composition
Silt		
Sand	30	<1
Gravel	10	<5
Stones	30	60
Boulders	30	30
Bedrock	<1	5

been observed after areas have been fished out (McCormick *pers. comm.*, Cranbrook 1976) it is our view that mussels previously buried, and so not removed, have pushed up into view.

When mussels first leave their fish hosts they are only 0·5 mm in diameter and probably establish themselves immediately in coarse sand. At this stage they (and the sand) may be redistributed passively by water currents and this method may contribute to the recolonisation of denuded areas. It has been suggested that mussels move most at very low water (Bauer *pers. comm.*), moving to deeper water to avoid becoming stranded, or to avoid warm deoxygenated water, however our evidence does not really support this contention. If there is a time of maximum movement it seems to be autumn which is certainly not a time of low, warm water in western Scotland. Instead we have often observed spates at that time of year.

Furthermore we have observed mussels being stranded and sometimes these have moved but sometimes not. Our evidence is insuficient to link movement with any special environmental factor.

We suggest that mussels are sedentary, by preference, if they find a suitable area of coarse sand in which to burrow and which remains stable. They do seem to burrow more deeply or more shallowly occasionally but the reasons for this are not clear and natural changes in the depth of the sand may contribute to the observation. However if the mussel's position becomes unsuitable, either due to low water, a change in the substrate or whatever else, then they have the capacity to move, at least short distances, to a new position. This movement is only possible across areas of suitable substrate except for the occasional involuntary washing out of mussels, and so recolonisation must depend mainly on invasion of young mussels from fish. Eager (1977) suggests that it is mainly mussels inhabiting the slower rivers which move and that their generally rounded and less 'beaked' shape (in relation to mussels from faster rivers) is more suitable for movement.

One factor influencing whether mussels persist in a stream is obviously the stability of the substrate in relation to the current speed and some otherwise suitable streams are clearly too torrential. Altnoder (1926) measured the gradient of various streams in Germany and found a good correlation between the gradient and the presence of mussels. In streams where the gradient averaged 2·36% mussels were absent, whereas in streams where they were present the average gradient was 1·36%. He does not suggest whether the effect of the increased gradient acts directly on the mussel or indirectly through instability of the substrate. This study suggests that a direct effect on the mussels may occur but, of course, the substrate may also be affected as well and this would have an indirect effect on the mussels which we have not attempted to measure.

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