THE INFLUENCE OF SEASON AND BARNACLES ON THE ALGAL COLONIZATION OF *PATELLA VULGATA* EXCLUSION AREAS

S. J. HAWKINS*

Department of Marine Biology, Liverpool University, Port Erin, Isle of Man

(Figs. 1–8)

Patella vulgata were excluded from barnacle dominated areas at Port St Mary, Isle of Man by wire fences attached to the rock in September 1977, December 1977, April 1978 and July 1978. The sequences of algal colonization of these exclusion areas differed markedly with season: in autumn diatoms were followed directly by *Fucus*, in winter and spring diatoms were followed by green algae and then *Fucus*, and in late summer *Fucus* sporelings arose directly on the barnacles. There was no evidence that the initial stages were necessary for the subsequent recruitment of *Fucus*.

Semibalanus (= *Balanus*) *balanoides* was scraped from half of the exclusion areas (with suitable controls) of a second series of experiments set up in October 1978, February 1979, April 1979. The pattern of algal colonization was very different in the scraped and unscraped halves of the exclusion areas. In the October experiment *Fucus* rapidly recruited directly on the barnacles, in contrast diatoms, green algae and a little *Fucus* recruited very slowly to the scraped half. In February and April *Ulothrix* directly colonized the scraped area, and was followed by *Blidingia*. *Blidingia* was directly recruited to the unscraped half. Diatoms were not so prevalent on the second set of experiments.

There was minimal algal growth in the controls of both sets of experiments.

INTRODUCTION

The importance of *Patella* grazing in regulating algal vegetation on moderately exposed British rocky shores was shown conclusively by the classical limpet removal experiments of the 1940s and 1950s done on the Isle of Man (Burrows & Lodge, 1950, 1951; Jones, 1948; Lodge, 1948; Southward, 1953, 1956, 1964). This has been confirmed by other experiments elsewhere (Aitken, 1962; Ballantine, 1961; Lewis & Bowman, 1975) and by observations on kills of grazers following dispersant application to oil-spills (see Southward & Southward, 1978 for full account of the 'Torrey Canyon' spill and review).

I decided to examine how season influenced algal colonization of barnacle-covered areas from which *Patella* were excluded on the Isle of Man. This had not been attempted on a systematic basis in the mid-tidal of a British shore before (but see Cubit, 1975 – who worked in the high intertidal in Oregon; Dayton, 1971 – in Washington; Menge, 1975 – in New England, all of whom worked with different grazers and, except in the last case, different algae).

The seasonal and other experiments (Hawkins, 1979) showed that sporelings of *Fucus* did not settle directly upon vacated limpet scars, areas of bare rock, nor areas scraped free of barnacles when *Patella* was excluded. Menge, (1975) reported that *Fucus* settles

* Present address: Department of Zoology, Manchester University.

more readily in crevices, on rough surfaces, and amongst barnacles both naturally and in exclusion areas. Further experiments therefore were started to test the effects of dense cover of the barnacle *Semibalanus* (= *Balanus*) *balanoides* (see Newman & Ross, 1976 for revision of barnacle taxonomy) on algal colonization of exclusion areas.

   Species are named according to the *Marine Fauna of the Isle of Man* (Bruce, Colman & Jones, 1963) and the latest algal check-list (Parke & Dixon, 1976).
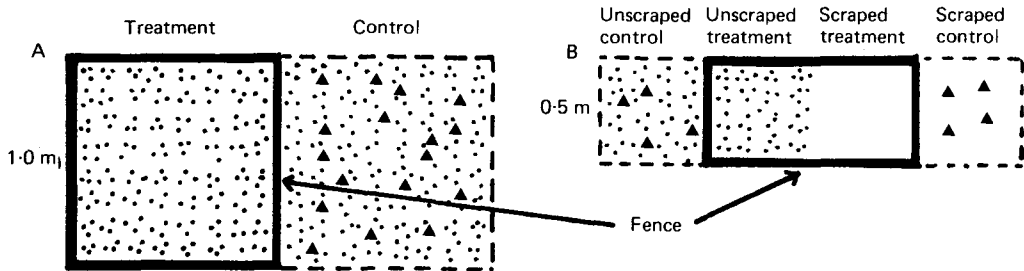

Fig. 1. Design of experiments. (A) Seasonal exclusion experiments. (B) Experiments testing the influence of barnacles. T, treatment; C, control; ▲, *Patella*; stipples, barnacles.

METHODS

Seasonal exclusions

   Experiments were set up at about 3-monthly intervals (21 Sept. 1977, 21 Dec. 1977, 16 Apr. 1978, 21 July 1978) on a gentle slope covered with *S. balanoides* at approximately M.T.L. on Port St Mary 'Ledges', Isle of Man (see Hawkins, 1979; Southward, 1953). Each experiment consisted of a 1 m² fenced exclusion area with an unfenced control area (see Fig. 1A). The fence was made from a strip of 12 mm, square-weld galvanized steel mesh, bent to give a 25 mm flange and 25 mm upright. These fences were fixed by 25 mm stainless steel screws in plugged 4·5 mm holes in the rock made with a drill powered by compressed air from SCUBA cylinders (Hawkins & Hartnoll, 1979). The *Patella vulgata* on the shore studied were large (see Fig. 2), so the coarse mesh size was sufficient to exclude them completely except after breakage or bending by storms. The matrix of *S. balanoides* inside the exclusion area was left intact. Control areas were not fenced with the *Patella* present inside, as it was felt that grazing pressure might be increased by restricting movements, or repeated encounters with fences might inhibit foraging. As the mesh size was wide, the exclusion areas large and situated on well-drained rock, any micro-environmental effects of the fences were expected to be minimal, and no allowance was made for this in the controls. The results of additional experiments on *S. balanoides*-dominated areas will be treated qualitatively to give a fuller picture of seasonal differences in algal colonization.

Influence of barnacles

   Experiments to test the effects of *S. balanoides* on algal colonization of exclusion areas were set up in a nearby homogeneous *S. balanoides*- and *Patella*-dominated community. A 1 × 0·5 m fenced exclusion area was constructed as before, but half the barnacles were scraped from it (see Fig. 1B). A 0·5 × 0·5 m area was scraped of barnacles next to the scraped half of the exclusion but with the limpets left in place to act as a control. An untouched area was designated as a further control next to the unscraped half of the exclusion. Experiments were set up at various times of the year (23 Oct. 1978, 22 Feb. 1979, 24 Apr. 1979) because of the previously shown importance of season in determining sequences of algal colonization.

   Patella removed from both sets of experiments were weighed and measured.

RESULTS

Seasonal exclusion experiments

P. vulgata were present in the experimental area at a very regular density of 25 ± 6 m^{-2} (mean and standard deviation of eight 1 m^2 control and treatment areas) and a biomass of 22 ± 2 g m^{-2} dry weight (mean biomass of *Patella* removed from 4 treatment areas). The length–frequency distributions and biomasses of the *Patella* removed from the
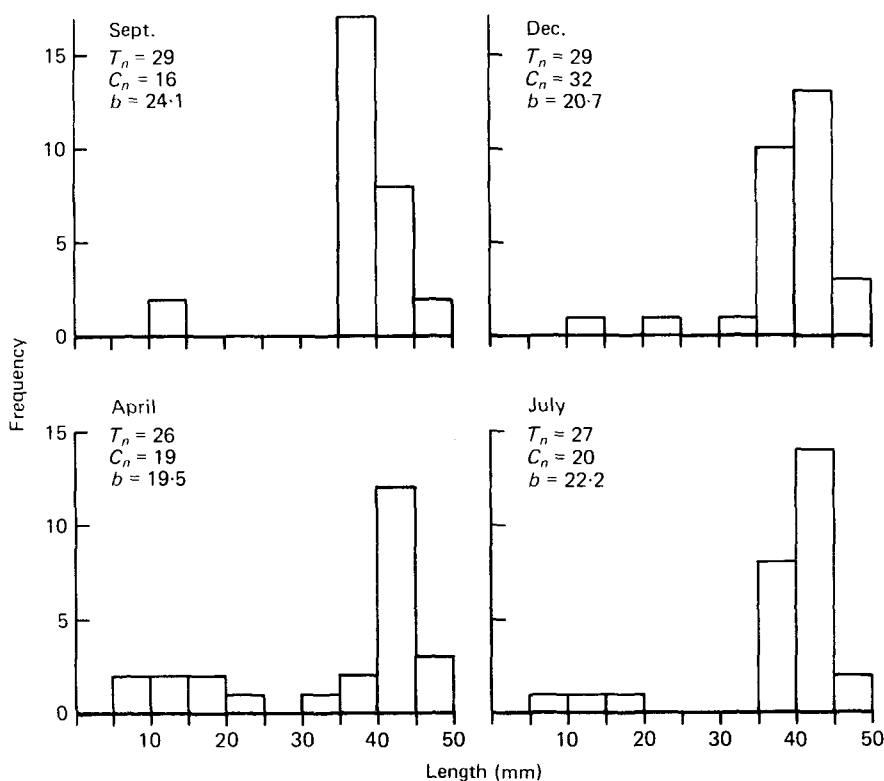

Fig. 2. Length–frequency distribution and biomass (dry wt.) of *Patella* removed from treatment areas. T_n, initial number of *Patella* in the treatment; C_n, initial number of *Patella* in the control; b, biomass, g m^{-2} dry weight.

exclusion areas (see Fig. 2) show that the whole experimental area had a homogeneous population structure. The controls and treatments had almost identical ($\sim 95\%$) cover of *S. balanoides*. In 3 out of 4 experiments there were fewer *Patella* in the controls than removed from the treatment areas (see Fig. 2); this, when the changes in the exclusion areas are considered, emphasizes the importance of even small numbers of limpets. The only *Fucus* present in September 1977 in the whole experimental area was growing on *Patella* shells or was very small sporelings (< 10 mm) (see Fig. 4A). Large *Fucus* plants were not present in any of the treatment or control areas at the start of each experiment.

September exclusion (Fig. 3A)

In the treatment there was an initial rapid growth of diatoms, which reached 80 % cover by mid-October. A minute amount of filamentous green algae also appeared. *Fucus* sporelings increased rapidly in the treatment, reaching 100 % cover by February, and subsequently forming a dense canopy (see Fig. 4B). *Actinia equina* and *Nucella lapillus* were found under this canopy 10 (July 1978) and 13 (Oct. 1978) months later respectively.
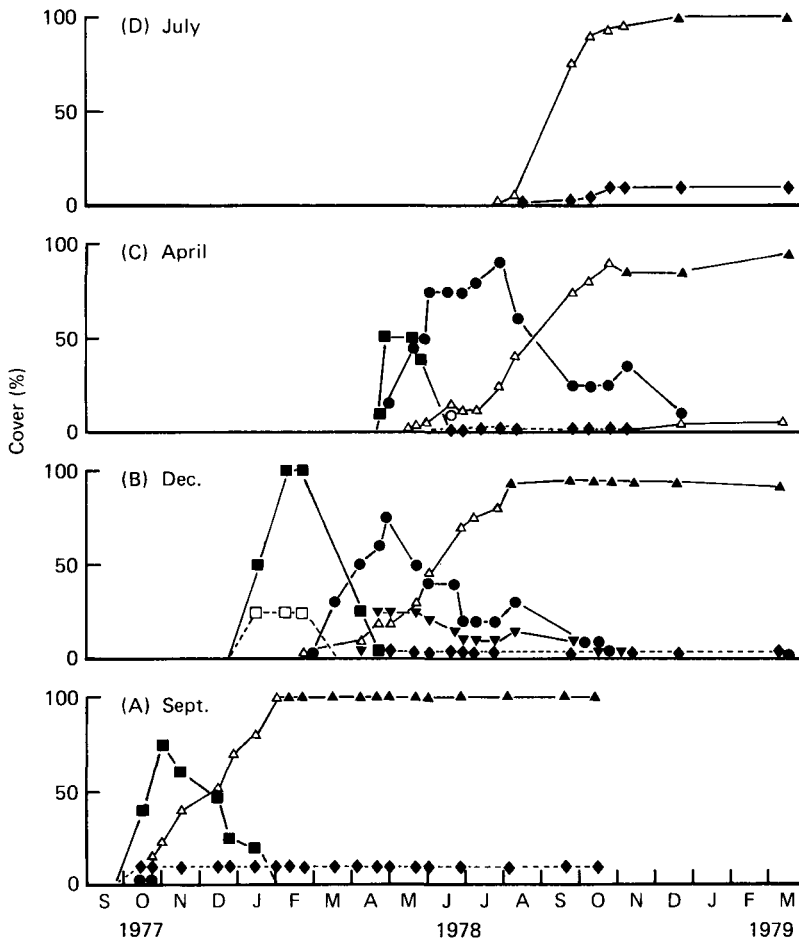

Fig. 3. Percentage cover of algae in the seasonal exclusion experiments set up in September 1977, December 1977, April 1978, July 1978. ■—■, Diatoms in treatment; □--□, diatoms in control; ●—●, green algae in treatment; ○—○, green algae in control; △—△, *Fucus*, sporelings occupying substrate space in the treatment; ▲—▲, *Fucus* occupying canopy space in treatment; ◆—◆, *Fucus* in the control; ▼—▼, *Porphyra* in the treatment.

Diatoms were not found in the control, but some *Fucus* sporelings managed to grow in a small part without *Patella* (see Fig. 4B). The plants reached 5 % cover and did not increase above this. *Actinia* and *Nucella* were not found in this small clump.

December exclusion (Fig. 3 B)

There was an initial diatom phase in the treatment, similar to, but denser than that described above which reached 100% cover by mid-January. Green algae followed (mainly *Enteromorpha* sp. and *Blidingia minima*, plus some *Monostroma* sp.) which overgrew the diatoms, reaching a peak of 80% cover in late April and early May. *Porphyra* sp. (probably *purpurea*) appeared in mid-February at the same time as the first greens, reaching a maximum of 30% in May. Both the *Porphyra* and green algae decreased as Fucus sporelings, which first appeared in March, increased in cover reaching 95% by August, and remained at about this level to the end of the experiment. *Actinia* and *Nucella* were first seen under the canopy 7 (July 1978) and 10 months (Oct. 1978) later respectively.

A small amount of initial diatom growth occurred briefly in the control during January 1978. A very few small *Fucus* sporelings appeared throughout the experiment.

April exclusion (Fig. 3 C)

The treatment showed a similar sequence to the December exclusion, except that the diatom phase was briefer and reached a lower peak. Green algae (mainly *Blidingia minima* and *Enteromorpha* spp.) quickly overgrew the diatoms and reached a peak of 90% cover by the end of July, subsequently decreasing to virtually zero by the end of the experiment. *Fucus* sporeling recruitment was slow at first in May and June, but rapidly accelerated in July, reaching 95% cover by October 1978. *Porphyra* sp. first appeared in May and occasional plants occurred until October. *Actinia* and *Nucella* were first observed under the canopy in December 1978 (9 months later).

Diatoms did not appear in the control; but some green algae did in June but soon vanished, presumably grazed. There were a few small *Fucus* sporelings in the control from June to November.

July exclusion (Fig. 3 D)

Fucus sporelings appeared in both the treatment and control shortly after the experiment started. Recruitment to the treatment was heavy, and cover increased rapidly; 90% cover was reached by the beginning of October. Some sporelings managed to grow in the control, probably because settlement was so great, thus permitting some 'escape' from *Patella* grazing. These reached 10% cover by November 1978, staying at this level to the end of the experiment. None of the diatom or green algal phases previously described occurred in the treatment. *Nucella* and *Actinia* were first found under the canopy in November 1978 (4 months later).

General comments

There was very little *Fucus* sporeling recruitment in all experiments once a dense canopy had been achieved. A second period of *Fucus* recruitment occurred after six months in the 'April' experiment under gaps formed by loss of plants. The rate of *Fucus* recruitment was fastest in the 'July' exclusion and slowest in 'December's' and 'April's'. The bulk of *Fucus* recruitment in 'April's' coincided with 'July's', though at a lower rate
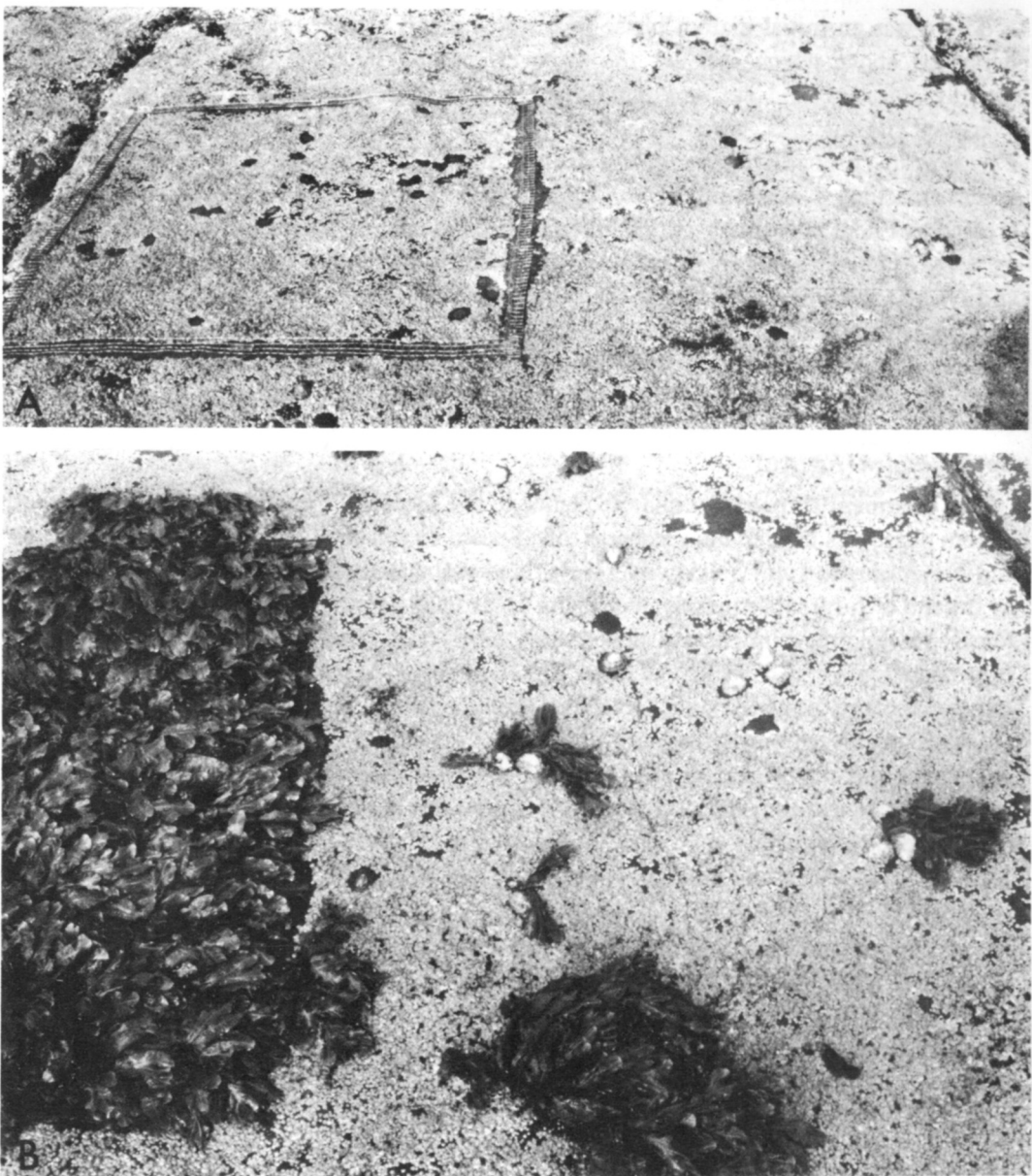
Fig. 4. Photographs of seasonal exclusion experiments. (A) Initial experimental set-up Sept. 1977. (B) Photograph of control area and half of treatment in April 1978.

T, treatment; C, control; E1, 'escape' of *Fucus* in control in September; E2, 'escape' having grown by April. The other *Fucus* present in the control in April is on limpet shells (S). F, *Fucus* in the control.

presumably due to the effects of already existing larger sporelings. The majority of sporelings grew into recognizable *F. vesiculosus* plants, with the exception of some strange forms, including those with marginal inflations, which seemed more common in the December and April exclusions. These may have been hybrids (see Burrows & Lodge, 1951), but more recent laboratory evidence suggests these are unlikely to occur in the wild (Bolwell *et al.* 1977). No identifiable *F. spiralis* or *F. serratus* plant was found.

Other experiments (see Hawkins, 1979)

A 2 m wide by 20 m long strip of rock from which *Patella* were removed in late February/early March 1977 showed a marked diatom phase followed by green algae and *Fucus*. Experiments set up to test the effects of *Patella* exclusion on *S. balanoides* settlement in late April 1977, mid-June 1977, mid-May 1978 and early May 1979 also all showed a marked green algal phase. However, diatoms were only seen in small amounts in April 1977. *Fucus* sporelings eventually grew in all the above areas.

Table 1. *Initial composition of treatment and control areas of experiment testing the effects of barnacle removal on algal colonization of exclusion areas*

	Semi Balanus removed				*Semi Balanus* present			
	Treatment		Control		Treatment		Control	
	⋆P	*⋆B*	*P*	*B*	*⋆P*	*⋆B*	*P*	*B*
22 Oct. 1978	4	95	5	95	3	95	6	95
22 Feb. 1979	5	95	3	90	4	95	5	95
24 Apr. 1979	4	95	5	95	5	95	3	90

Average *Patella* density ~ 17 m^{-2}, biomass 14·4 g m^{-2}.
⋆ $P = $ *Patella* no. per 0·25 m^2, $B = $ barnacle % cover.

Influence of barnacles

Table 1 gives the original composition of the experimental areas. The whole experimental area had 90–95 % *S. balanoides*, and the only *Fucus* present at the start of each experiment were a few small sporelings. In all experiments there were considerable differences in algal colonization of the two halves of the exclusion area.

October exclusion (*Fig. 5*)

There was no significant growth of algae in either the *S. balanoides*-scraped or *S. balanoides*-present controls. A very few *Fucus* sporelings were observed in the latter but rapidly disappeared, presumably due to *Patella* grazing.

On the scraped half of the exclusion (see Fig. 5A) diatoms grew quickly, reached a peak by December, and declined as they were replaced by green algae. Initially there were some filamentous greens (*Ulothrix* or *Urospora*), but subsequently virtually all the algae was *Enteromorpha intestinalis*. This rapidly achieved almost total cover, but decreased after reaching 100% as *Porphyra purpurea* steadily increased to over 50% cover (see Fig. 6). *Fucus* sporelings first appeared in February, but recruited slowly, reaching only 5 % cover by the end of September.
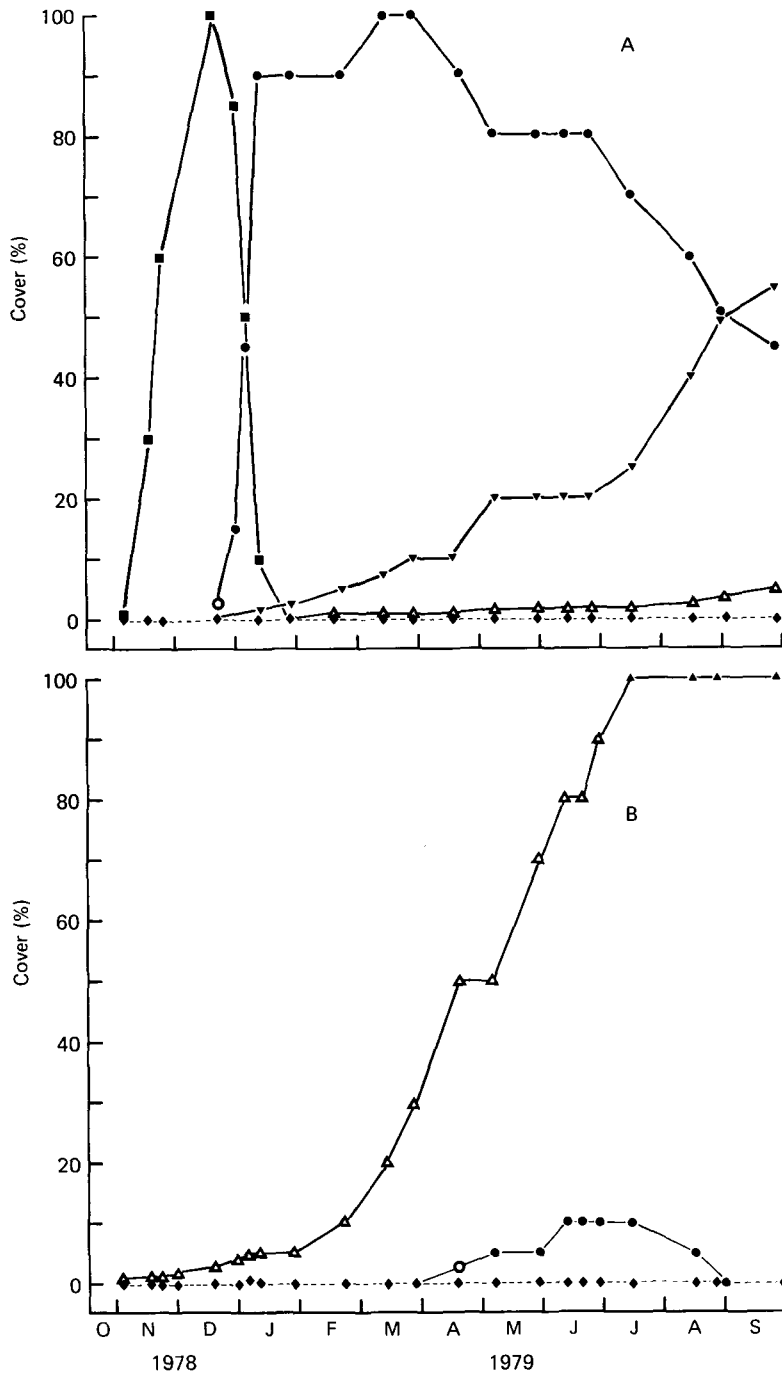
Fig. 5. Percentage cover of algae in October experiment testing the effects of barnacles on algal colonization of exclusion areas. (A) Scraped exclusion plus control. (B) Unscraped exclusion plus control. ■—■, Diatoms; ○—○, *Ulothrix* and other small green filamentous algae; ●—●, *Enteromorpha intestinalis*; ▼—▼, *Porphyra*; △—△, *Fucus* sporelings occupying substrate space in the treatment; ▲—▲, *Fucus* occupying canopy space in the treatment – all in treatment; - - ◆ - -, total algae in controls.
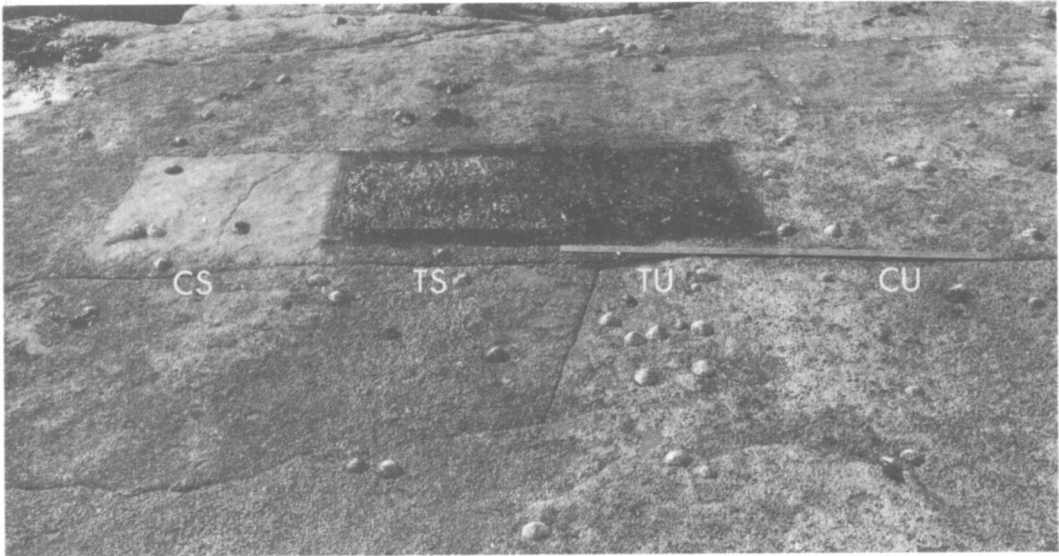
Fig. 6. Photograph of the October 1978 *Patella* exclusion experiment testing the influence of barnacles taken in April 1979. CS, Scraped control without algae; CU, unscraped control; TS, scraped treatment covered with *Enteromorpha* plus some *Porphyra*; TU, unscraped treatment half-covered by *Fucus* sporelings.
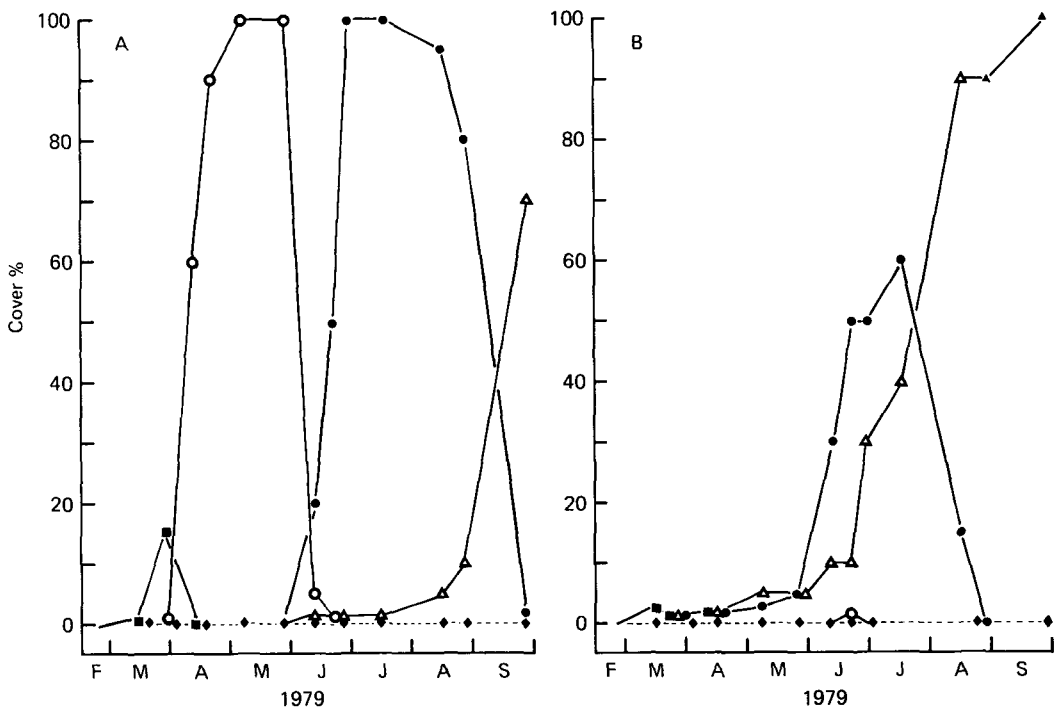

Fig. 7. Percentage cover of algae in February experiment testing the effects of barnacles on algal colonization of exclusion areas. (A) Scraped exclusion plus control. (B) Unscraped exclusion plus control (symbols as Fig. 5 except ●—●, *Blidingia minima*).

Fucus sporelings appeared immediately in the *S. balanoides*-covered half of the exclusion area (Fig. 5 B), steadily increasing in cover (see Fig. 6) and reaching 100 % by July 1979. Diatoms were not observed at all, and green algae did not appear until April. Then some *Ulothrix* sp. colonized the bare rock of an erstwhile limpet scar, and soon afterwards some *Blidingia minima* appeared under the dense stand of *Fucus* sporelings, gradually disappearing by September.
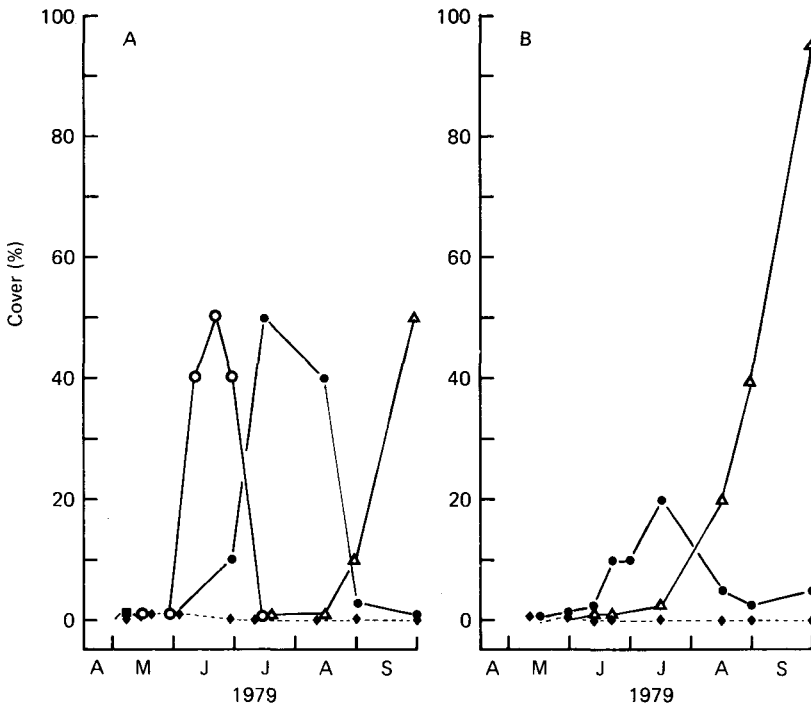

Fig. 8. Percentage cover of algae in April experiment testing the effects of barnacles on algal colonization of exclusion areas. (A) Scraped exclusion plus control. (B) Unscraped exclusion plus control (symbols as Fig. 7).

February exclusion (Fig. 7)

Virtually no algal growth occurred on either control area.

The scraped half of the exclusion area (see Fig. 7 A) showed a small initial diatom peak, which was rapidly superseded by growth of the filamentous green alga, *Ulothrix* sp. This achieved maximum cover in early May, but died off by early June, perhaps in direct response to a spell of hot weather. *Blidingia minima*, which replaced it, only increased rapidly in cover after *Ulothrix* had virtually disappeared, reaching total cover by mid-July. A few *Fucus* sporelings were observed in June and July, initially increasing slowly in cover until late August and September; afterwards cover rapidly increased. *Blidingia* rapidly decreased at the same time.

Fucus sporelings, *Blidingia*, and some colonial diatoms all appeared at the same time on the *S. balanoides*-covered half of the treatment (Fig. 7 B). The diatoms quickly

disappeared. The cover of both *Fucus* and *Blidingia* increased at the same time, the latter slightly faster until mid-July. Then *Blidingia* rapidly decreased as *Fucus* increased in cover to 90 % by mid-August.

April exclusion (Fig. 8)

Some algae briefly appeared in the controls of this experiment. There was a slight green tinge (small filamentous and unicellular algae) on the bare rock control, and a small amount of *Blidingia* (< 2 %) on the *S. balanoides*-covered control. This was probably attributable to the large amount of green algal spores present at this time of year. The algae in both controls were soon grazed away by *Patella*.

In the scraped exclusion (Fig. 8A) *Ulothrix* quickly colonized the surface to reach a peak in mid-June, then died off as it was replaced by *Blidingia*. A few *Fucus* had appeared by July, which rapidly increased in cover in September, *Blidingia* correspondingly decreasing.

Blidingia directly colonized the *S. balanoides*-covered exclusion area (Fig. 8B) reaching 20 % cover by July, but decreased as *Fucus* sporelings increased in cover. Some *Porphyra* also appeared in small amounts.

Other observations

In a nearby exclusion experiment (set up in April 1979) testing the effects of *Patella* on *S. balanoides* settlement (see Hawkins, 1979), *Ulothrix* directly colonized the bare rock of small scraped settlement squares (0·10 × 0·10 m), whilst *Blidingia* directly colonized the surrounding barnacle matrix.

DISCUSSION

Southward & Southward (1978) suggest a 'regular succession' of algae that followed experimental removal or massive kills of *Patella* on West British shores. There is an initial transitory phase of diatoms, unicellular and filamentous algae often only apparent in autumn and winter; this is followed by a green algal flush of principally *Enteromorpha* spp. of varying duration, which is in turn succeeded by *Fucus* sporelings. This summary was based on their observations and those of other workers (Aitken, 1962; Burrows & Lodge, 1950; Jones, 1946, 1948; Lodge, 1948; Southward, 1953, 1956, 1964) following death or removal of limpets in winter or spring from barnacle-covered rocks.

The exclusion experiments set up in December 1977 and April 1978 on barnacle-covered areas agree with the above summary. However, the September 1977 and July 1978 exclusions clearly demonstrate how the observed sequences of algal colonization can vary with season. Diatoms appeared first from October to April. Green algae followed them from January to April, but could occur first from April to June (shown by the various qualitatively treated experiments). In spring and summer the green algae were primarily *Blidingia minima*, which is easily confused with *Enteromorpha* spp. in the field, and was once classed as *Enteromorpha*. This may explain why it was not recorded by some earlier workers, or included in Southward & Southward's summary. *Fucus* sporelings were recruited all year round, but most strongly just after the main fruiting period of *F. vesiculosus* (May to July – Knight & Parke, 1950). The *Fucus* phase followed either the

initial diatom stage in autumn, or the green algae in winter/spring, or arose directly on the barnacles in July and August.

The algae colonizing the exclusion areas cleared of all barnacles showed Southward & Southward's general pattern. Unfortunately a summer experiment was not set up. According to season some of the earlier stages of their pattern were bypassed on the adjacent *S. balanoides*-covered half of the exclusion area. The results roughly agreed with the previous year's seasonal exclusion experiments, the only difference being that the diatom phase was not so marked on the unscraped treatments set up in October 1978, and February 1979 as in those of September and December 1977. This indicates that the extent and season of diatom recruitment can vary considerably between years (see Jones *et al.* 1979).

Various explanations are possible for the marked differences between the scraped and unscraped halves of the experiments. The large numbers of small snails (< 3 mm), mainly *Littorina neglecta* Bean, present amongst the barnacle shell matrix (about 4000 m^{-2} ~ 4 g m^{-2} shelled dry weight) may exert a considerable grazing pressure. They might selectively feed on green algal sporelings and diatoms, preventing their growth except at certain times of the year (see Menge, 1975; Lubchenco, 1978 for work with 'L. saxatalis' and *L. littorea*). Unfortunately they cannot be easily excluded without drastically altering the environment. Green algae only grew in the middle of small barnacle settlement squares scraped within the barnacle matrix of an exclusion area. Their absence from the edge was probably due to forays of small *Littorina* from amongst the barnacles.

Alternatively the feeding activities of barnacles may selectively remove the smaller diatoms and green algal spores, but miss the larger, heavier *Fucus* eggs. This seems unlikely (see Crisp, 1964). I attempted to test this by killing and fixing barnacles intact *in situ* using injections of 70% alcohol. The 0·10 × 0·10 m area treated in this way showed no discernible difference from the rest of the exclusion. This probably indicates that barnacle feeding was not responsible for the difference, though the treatment may have failed in some way.

Barnacle shells are heavily impregnated with burrowing algae (Parke & Moore, 1935) including some species of green algae which have burrowing phases of their life history (C. Van der Hoek, personal communication). These, plus spores lodged in cracks and crevices amongst the barnacles, would provide a reservoir for immediate recruitment if grazing was removed. The scraped areas would need to be colonized from remote sources. This may explain the development of *Blidingia* directly on the barnacle shells; whilst the smaller alga *Ulothrix* initially colonized the scraped area, *Blidingia* eventually following afterwards on the latter. Competition with *Blidingia* (see Hruby & Norton, 1979), *Littorina* grazing, or unsuitability of the substrate may have prevented growth of *Ulothrix* on the barnacles.

On barnacle-covered rock sequences of algal colonization seem wholly determined by availability of propagules, which varies both seasonally and between years. Previous colonization by diatoms or small filamentous algae is not essential for the establishment of larger green algae such as *Blidingia* and *Enteromorpha*. These in turn are not a prerequisite for successful recruitment and growth of *Fucus*. Thus preliminary or 'pioneer'

stages (see Connell & Slatyer, 1977 for review of succession including terminology), can be by-passed on the barnacles as the rough surface aids recruitment of *Blidingia* and *Fucus*.

Conversely, on the scraped halves of the exclusion areas there is some evidence that preparatory stages of diatoms and *Ulothrix* are necessary for the subsequent colonization of larger green algae and *Fucus* (Hatton, 1938; Moore, 1939). Paradoxically, the dense felt of *Enteromorpha intestinalis* and latterly *Porphyra purpurea* in the scraped half of the 'October' exclusion seemed to inhibit *Fucus* recruitment, as only a very few sporelings had appeared and grown 10 months later. Menge (1975) also reported that *Fucus* was out-competed by *Enteromorpha* in short-term experiments.

The controls showed that during the period of study the balance between algal recruitment and growth, and *Patella* grazing, was generally tilted in favour of the limpets. However, at certain times of the year algae were briefly able to recruit and grow in the controls. The diatoms in winter and the green algae in spring did not last long; presumably because their susceptibility to limpet grazing does not decrease as their size increases. *Fucus*, however, does become less susceptible (see Burrows & Lodge, 1951; Southward, 1956), and from July to October most natural recruitment occurs through 'escapes' from grazing.

The importance of *S. balanoides* in facilitating *Fucus* 'escapes' is emphasized by the differences in recruitment rate to scraped and unscraped exclusions. The barnacles provide a suitable settlement surface and small refuges from grazing during germination in the gaps between them. There is considerable recruitment of algae to areas of old, dense senescent barnacles, irrespective of the density of *Patella* (Hawkins, 1979). This is attributable to the more numerous and deeper crevices, and the more uneven surface, which presumably restrict the extent and effectiveness of the limpets' foraging. *Fucus* 'escapes' are not so likely on areas of bare rock even if grazing pressure lessens as intermediate green algal stages seem necessary for *Fucus* sporeling establishment. Green algae are vulnerable to *Patella* grazing, and some species such as *E. intestinalis* are able to persist and probably competitively exclude *Fucus* sporelings in at least the short term. Thus there may not be time for an 'escape' of *Fucus* on bare rock prompted by a short-lived local reduction in grazing intensity.

Escapes of *Fucus* from grazing in areas of lower limpet density on barnacle-covered rock are primarily responsible for the observed small-scale patchiness on moderately exposed shores on the Isle of Man and elsewhere (see Hawkins, 1979 for further discussion). Irregular predation by seabirds and perhaps fish, physical disturbance and often human interference can all reduce *Patella* locally (see also Southward & Southward, 1978). On Manx east coast shores escapes are further facilitated by overall low densities of limpets and low levels of recruitment (see Hawkins, 1979) plus their generally aggregated spatial distribution (Hartnoll & Hawkins, 1980).

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