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Settlement and post-settlement interactions between *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) and three species of fucoid canopy algae

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Abstract

Manipulative field experiments carried out on sheltered rocky shores investigated settlement and post-settlement interactions between *Semibalanus balanoides* and three species of fucoid canopy algae, *Fucus spiralis* L., *Ascophyllum nodosum* (L.) Le Jolis and *Fucus serratus* L. All three species had a negative effect on settlement and early recruitment of *S. balanoides*, densities being significantly lower on settlement tiles beneath the canopy compared to cleared areas. Investigation of the mechanism by which settlement and recruitment were inhibited showed the importance of sweeping of algal fronds at all three shore heights. In addition, we found that the *F. serratus* canopy inhibited settlement not only by its sweeping action but also by limiting the access of cyprids to the substratum. Detailed examination of the sweeping effect in *F. serratus* showed that newly settled cyprids transplanted beneath a canopy suffered extremely high mortality (between 82 and 97%) over just one high water period. Mortality was significantly reduced for individuals that had settled within a matrix of adults. Metamorphosis of cyprids to spat conferred no additional resistance to sweeping-induced mortality but resistance increased in 6 day old spat. Mortality in *S. balanoides* after the end of the settlement season was monitored for three months in experimental treatments and controls. Mortality rates were significantly lower under the canopy than in cleared areas in both the *F. spiralis* and *Ascophyllum* zones. The overall influence of each canopy species on the development of barnacle populations on sheltered shores is discussed.

Keywords: Fucoid canopy; Rocky intertidal; Recruitment; *Semibalanus balanoides*; Settlement; Sheltered shore

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1. Introduction

Sheltered, canopy-dominated shores of north-west Europe are characterised by a low abundance of barnacles (Moore, 1935; Stephenson and Stephenson, 1949; Lewis, 1964; Hawkins et al., 1992). At many sheltered sites, barnacles only occur on steep seaward facing slopes and in the high shore *Fucus spiralis* zone. The importance of wave action (e.g. Vadas et al., 1990) and grazing (Jones, 1948; Southward, 1964; Southward and Southward, 1978; Hawkins et al., 1992) in preventing extension of fucoids into exposed shores has been long understood. Much less is known about what prevents barnacles and limpets from extending onto sheltered shores.

One of the main factors affecting barnacle abundance at sheltered sites is likely to be interactions at settlement between cyprids and the macroalgal canopy. Hatton (1938) first demonstrated a negative effect of fucoids on the recruitment of *Semibalanus balanoides* and attributed this to the reduction of water circulation beneath a canopy, resulting in a limitation of larvae coming into contact with the substratum. Most work subsequent to this has considered the sweeping action of algal fronds across the substratum surface to be the main cause of recruitment limitation, settling or settled cyprids being destroyed or simply swept away (e.g. Menge, 1976; Grant, 1977; Hawkins, 1983). Menge (1976), working on the east coast of North America, demonstrated this experimentally; enhanced recruitment by *S. balanoides* beneath a *Fucus vesiculosus* and *Ascophyllum nodosum* canopy was achieved by protecting the substratum with roofs and cages. The degree to which recruitment is affected by sweeping may depend on a number of factors, including the degree of wave exposure and the species of canopy alga. Hawkins (1983) concluded that on moderately exposed shores *Fucus* sweeping inhibits settlement at all shore levels while at sheltered sites inhibition only occurs in the *Fucus serratus* zone. On the high shore it was found that although the fucoid canopy of *F. spiralis* and *F. vesiculosus* reduced cyprid settlement, this effect was less pronounced than the enhancement of post-settlement survival. A similar effect was observed by Dayton (1971). Settlement of *Balanus glandula* was not reduced under *Fucus distichus* and it was concluded that the canopy had a positive effect on recruitment owing to its ability to reduce desiccation.

The aim of this study was to investigate the importance of dense macroalgal canopies in determining the abundance of barnacles on sheltered shores. One major difficulty in the investigation of interactions between barnacle cyprids and the macroalgal canopy on sheltered, canopy-dominated shores, is the scarcity of adult barnacles on the substratum. Laboratory studies have demonstrated that cyprids of a number of barnacle species settle more readily on surfaces bearing settled conspecifics or treated with extracts of conspecifics than on bare untreated controls (e.g. Knight-Jones and Stevenson, 1950; Knight-Jones, 1953). This phenomenon has also been observed under natural conditions in the field (Hawkins, 1983; Raimondi, 1988). Hawkins (1983) showed that recruitment of *S. balanoides* into cleared areas in the *Ascophyllum* zone of a sheltered shore only occurred after stones bearing live adult barnacles were transplanted there. In order to determine if the presence of macroalgal canopies results in low barnacle populations and hence a low settlement stimulus it is necessary to transplant settlement surfaces which are attractive to settling cyprids to the experimental site.

Three separate experiments were carried out using settlement tiles made from barnacle encrusted natural rock. Experiments 1 and 2 tested the general hypothesis that macroalgal canopies cause a reduction in settlement and recruitment of *S. balanoides* on sheltered shores. In addition, these experiments examined the process by which inhibition of recruitment occurs. Canopy algae may interact with settling cyprids while still in the water column by forming a barrier to cyprid movement, and at settlement by sweeping across the substratum. The barrier effect has not been investigated in the past owing to the difficulty in separating its effect from that of sweeping. Manipulative field experiments were designed which distinguished between the sweeping effects of algal fronds on the substratum and the canopy acting as a barrier to cyprid movement. These experiments were carried out at three different shore levels within distinct zones of different canopy algae to test the hypothesis that the effect of macroalgal canopies on barnacle recruitment differs with shore height. The experimental design did not allow us to determine whether differences were due to changes in the algal species or the physical factors associated with height on the shore. In addition to interactions at settlement, the influence of the canopy on early post settlement mortality was examined to test the hypothesis that canopy algae can enhance survival of settled barnacles.

Results from experiment 1 demonstrated the importance of sweeping of algal fronds in limiting recruitment beneath macroalgal stands. Therefore a third experiment was designed to examine levels of mortality due to sweeping and specifically test the hypothesis that metamorphosis of cyprids to spat allows escape from sweeping induced mortality.

2. Methods and experimental design

Three separate experiments were carried out at sheltered, rocky intertidal sites on the Isle of Man, UK, to investigate the interactions at settlement between *Semibalanus balanoides* and the three different species of macroalgal canopies. Experiments 1 and 2 were carried out on a gently sloping sheltered shore on the west side of Castletown Bay which is dominated by dense stands of macroalgal canopies. Experiment 3 was carried out at a semi-sheltered site in Port Erin Bay.

Preliminary work on the attractiveness of different surfaces to settling cyprids showed negligible settlement onto artificial tiles or natural substrate lacking adult barnacles. Therefore settlement 'tiles' made from natural, barnacle encrusted rock were made. Large fragments of slate were chiselled from the mid-tide level of a moderately exposed shore dominated by *S. balanoides*. The settlement surfaces had a minimum size of 13×13 cm with a minimum barnacle cover of 50%. Tiles were stored in sea water and the cover of adult barnacles within the central 12×12 cm was manipulated to produce a cover from 33% to 50%. This was done in such a way as to produce a patchy distribution of adult barnacles and bare rock. One quarter of the tiles was selected at random and cages constructed over them. Cages were made from plastic coated chicken wire (mesh size 13×13mm) and were designed to form a complete cover over the whole tile with a 'roof' 3–4 cm above the settlement surface. Cages prevented any sweeping of algal fronds over the tile surface.

2.1. Experiment 1: Castletown Bay 1993

A factorial experiment was designed to investigate the effect of canopy sweeping, canopy barrier and shore height on *S. balanoides* settlement and recruitment. The factors canopy sweeping and canopy barrier had 2 levels, presence and absence (see Table 1). Unfortunately, treatment 3, where the canopy was cleared and a single large plant was left in the middle of each plot did not work as planned. Observation of this treatment on incoming and outgoing tides showed that in the relatively calm waters of the sheltered site, individual plants at the centre of each plot were affecting only a fraction of the settlement tiles. Thus, this treatment could not be considered effective and was rejected. The remaining three treatments were replicated in the high (5 m above Lowest Astronomical Tide), mid (4.1 m above L.A.T.) and low shore (2.8 m above L.A.T.). Each of the shore heights corresponded to the middle of three zones of macroalgae, *Fucus spiralis* on the high shore, *Ascophyllum nodosum* on the mid shore and *Fucus serratus* on the low shore. All three species of algae formed a dominant, near 100% cover over a distinct zone on the shore. Each treatment was replicated four times at each of the three shore heights. Within each replicate plot, four settlement tiles were used. These four tiles were treated as subsamples and used to calculate a mean value for each replicate. No cage-controls were used in this experiment. However, this matter was addressed in experiment 2.

A stretch of shore approximately 100 m long was chosen at the Castletown Bay site. At each shore level sixteen plots were selected. Experimental treatments were assigned at random to these plots, such that each treatment was replicated four times at each shore level. Canopy algae were completely cleared from a 2×2 m area in the appropriate plots. On April 27th, 1993, when cyprid settlement had commenced, tiles were transported to the experimental site. Four tiles were distributed within each experimental plot and fixed to the substrate using quick-setting cement. Tiles were positioned in slight depressions, to minimise raising of the tile surface above the surrounding substratum. In this way, each of four treatments was replicated four times at three shore levels, with each replicate containing four sub-samples.

The intensity of settlement to the different treatments was investigated by counting the number of settled cyprids on tiles within a 12×12 cm quadrat at one date during the main settlement period. Recruitment was measured by counting the number of

Table 1
Summary of treatments in experiment 1

Canopy barrier	Canopy sweeping	
Present	Present 1 Control Canopy intact	Absent 2 Caged Canopy intact Settlement tiles caged
Absent	3 Sweeper Canopy cleared Large single plant at centre of plot	4 Cleared Canopy cleared

metamorphosed individuals at three dates through the settlement season. Analysis of recruitment was performed on data from the final sampling date, June 2nd. Sampling was also undertaken on natural substrata to allow an assessment of recruitment levels onto sheltered shores under natural conditions of very low adult barnacle abundance.

After settlement had ceased, sampling of metamorphosed recruits was undertaken on three more occasions to investigate the effect of the canopy on post-settlement mortality. Monitoring occurred throughout the summer until tiles were fouled by ephemeral algae.

2.2. Experiment 2: Castletown Bay 1997

Experiment 1 was repeated in a modified form in May 1997 to examine more closely the hypothesis that macroalgal canopies act as barriers to cyprid access to the substratum. Experimental work was carried out at the same three shore heights as in experiment 1. Settlement of cyprids to caged tiles under the canopy was compared with settlement to tiles (both caged and uncaged) in areas cleared of canopy. The use of both caged and uncaged tiles in cleared plots in this experiment controlled for possible artefacts associated with the cages, a procedure lacking from experiment 1. Results from experiment 1 showed that variation between individual tiles used as subsamples within each replicate plot was low. Therefore in experiment 2 only one settlement tile was used in each single replicate plot. This allowed an increase in the level of replication, with each of the three treatments replicated six times within the three shore heights.

In this experiment the potentially confounding effect of differential post-settlement mortality between tiles under the canopy and tiles in cleared areas was minimised by only sampling for settlement over discrete 24 h periods. On three separate occasions all settled barnacles were cleared from the tile surfaces and the number of settled cyprids determined after 24 h. No examination of recruitment over longer time scales was made. Owing to problems of dependence between sampling dates (treatments were located in the same position on all dates) statistical analysis was only carried out on data from the first sampling date.

2.3. Experiment 3: Port Erin 1994

This experiment investigated the susceptibility of newly settled barnacles to sweeping by fronds of *F. serratus* and determined if metamorphosis of cyprids to spat changed the ability of an individual to survive sweeping. Different age classes of cyprid and spat were transplanted beneath a *F. serratus* canopy and into cleared areas and survival determined after one high water period. The three age classes of juvenile barnacles used were:

- Cyprids – transplanted immediately after settlement. When sweeping occurred they had been attached to the rock surface for between 6 and 12 h
- Newly metamorphosed spat – transplanted immediately after metamorphosis from the cyprid stage had occurred. When sweeping first took place they had been attached to the rock surface for between 30 and 36 h

- 'Old' spat – transplanted 6 days after metamorphosis and had thus been attached to the rock surface between 174 and 180 h before sweeping took place.

Settlement tiles made from natural barnacle encrusted rock were prepared as described above. On the majority of tiles (subsequently referred to as smooth) an area measuring at least 12×12 cm was cleared of adult barnacles. On the remaining tiles (referred to as rough), adult barnacles were removed individually to create small patches of bare substrate (< 1 cm^2 in size) within a mosaic of barnacles. Each tile was numbered individually and marked with enamel paint to permit relocation of the sampling quadrat.

Tiles were cemented onto boulders at mid shore level on June 9th, 1994 and brushed thoroughly to remove any newly settled barnacles. After one period of high water, the position of all newly settled cyprids was recorded on pieces of perspex placed over the tiles. New tiles were placed at mid shore level on three further dates, (June 10th, June 15th and June 16th) to allow cyprid settlement and so produce individuals of the age required for experimentation. Tiles were transplanted to the low shore *F. serratus* zone in three separate experiments (see Table 2). In all experiments the individually recorded barnacles were subjected to one high water period before being re-sampled at the following low water. Mortality was assumed by the absence of an individual.

2.4. Statistical analysis

Analysis of variance (ANOVA) was used throughout to test for treatment effects, with all factors in all experiments being treated as fixed. Cochran's test (Winer, 1971) was used to test for heterogeneity of variance and, where necessary, data were square root or arc-sin transformed. Multiple comparisons of levels within significant factors were made using Student Newman Keuls (SNK) tests.

Table 2
Summary of experiment 3

Experiment	Age class of barnacle	Treatments	Number of replicates	Time of sweeping	Sea state
A	Cyprid	Beneath canopy	5	June 10th	Rough
	Cyprid	In cleared areas	5	HW = 12.26 am	
	Cyprid	Rough tiles beneath canopy	5		
B	Cyprid	Beneath canopy	6	June 11th	Intermediate
	New spat		6	HW = 1.00 am	
	Cyprid	In cleared areas	6		
	New spat		6		
C	Cyprid	Beneath canopy	5	June 17th	Calm
	New spat		5	HW = 5.00 am	
	Old spat		5		

Unless otherwise stated tiles are smooth.

3. Results

3.1. Experiment 1: Castletown Bay 1993

3.1.1. Settlement

Settlement of cyprids varied significantly between the three canopy treatments and between shore heights (Table 3a, Fig. 1). There was a consistent ranking in levels of cyprid densities in the different canopy treatments at all shore heights; settlement was highest in cleared plots and lowest in control plots where tiles were subject to both the sweeping and barrier effect of the overlying algae. The caged tiles placed beneath the canopy but protected from the sweeping of algal fronds by cages showed intermediate levels of settlement. Student Newman Keuls multiple comparisons showed significant differences between all three canopy treatments (Table 3a).

A comparison of settlement between the three shore heights averaged over all three treatments shows that cyprid numbers were significantly higher in the high shore *Fucus spiralis* zone (Table 3a).

3.1.2. Recruitment

The number of metamorphosed recruits was monitored throughout the *Semibalanus balanoides* settlement season during which there was a cumulative increase in the number of individuals. After the settlement season, the decline in number of recruits was monitored for three months to assess the effect of the canopy on post-settlement mortality. Our division between the period of 'recruitment' and the period of post-settlement mortality does not imply post-settlement mortality did not occur during the

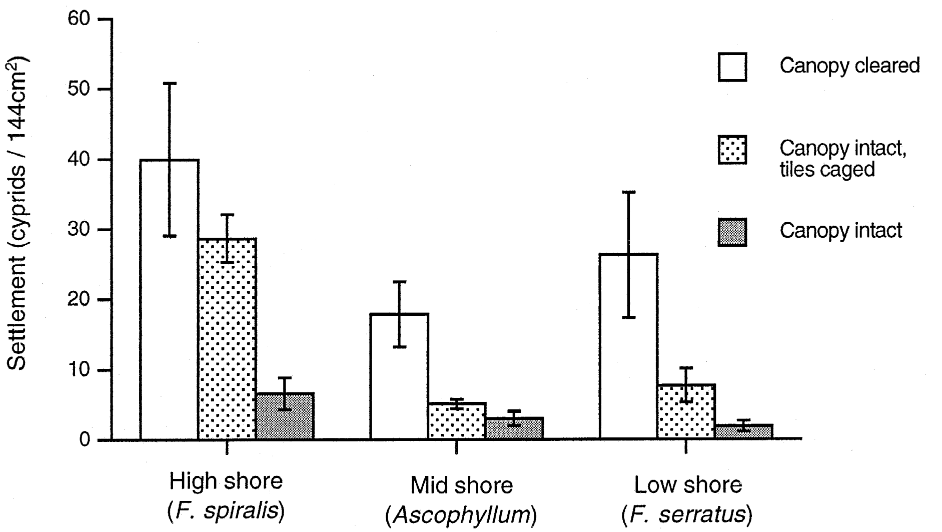

Fig. 1. Experiment 1: Mean number (± SE) of *S. balanoides* cyprids present on settlement tiles on one sampling date (22.5.93) during peak settlement.

Table 3
Two way ANOVA and SNK multiple comparisons of square root transformed data testing for the effect of canopy treatments and shore height in experiment 1. (a) Settlement of *S. balanoides* cyprids on 22nd May 1993. (b) Recruitment of *S. balanoides* on 2nd June 1993

	(a)				(b)			
Source	df	MS	*F*	*P*	df	MS	*F*	*P*
Canopy treatment	2	33.12	28.37	< 0.0001	2	491.54	31.99	< 0.0001
Shore height	2	13.75	11.77	< 0.0002	2	116.46	7.58	< 0.0024
Treatment × Height	4	1.68	1.44	> 0.25	4	28.29	1.84	> 0.15
Residual	27	1.17			27	15.36		
SNK multiple comparisons	Canopy treatment				Canopy treatment			
	Control v Caged	S			Control v Caged	S		
	Control v Cleared	S			Control v Cleared	S		
	Caged v Cleared	S			Caged v Cleared	NS		
	Shore height				Shore height			
	F. spiralis v *Ascophyllum*	S			*F. spiralis* v *Ascophyllum*	S		
	F. spiralis v *F. serratus*	S			*F. spiralis* v *F. serratus*	S		
	F. serratus v *Ascophyllum*	NS			*F. serratus* v *Ascophyllum*	NS		

settlement season. Patterns of recruitment over this period obviously represent a balance between input of barnacles from settlement and loss due to mortality, both of which may have been affected by the experimental treatment.

The recruitment of *S. balanoides,* like settlement, varied significantly between canopy treatments and between shore heights. Densities of spat were lowest in the control treatment at all three shore heights, thus reflecting the low settlement observed there (Fig. 2). The control was significantly lower than the other two treatments (SNK tests,

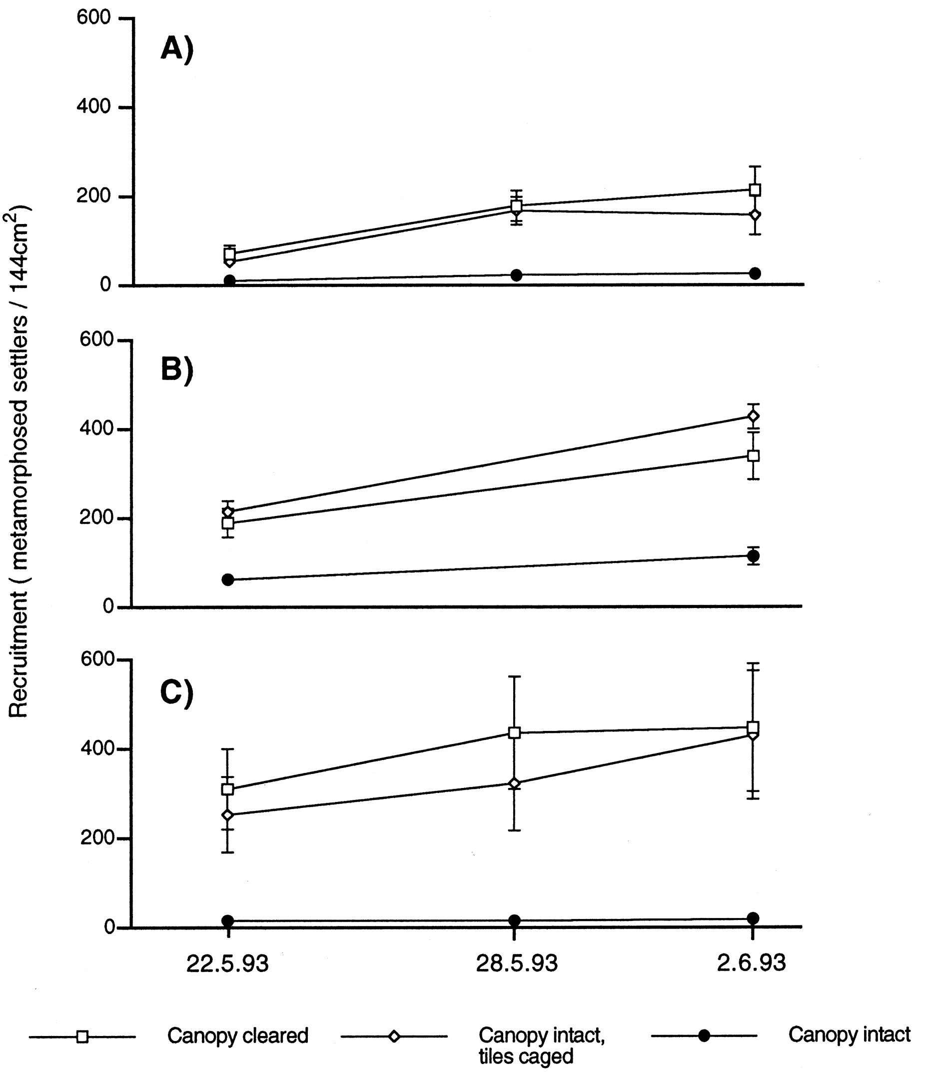

Fig. 2. Experiment 1: Mean number (± SE) of metamorphosed individuals (recruitment) of *S. balanoides* present on settlement tiles during period of settlement season. (A) High shore *F. spiralis* zone. (B) Mid shore *Ascophyllum* zone. (C) Low shore *F. serratus* zone.

Table 3b). In the caged treatment, recruitment did not appear to reflect settlement as high recruitment levels (equivalent to cleared plots) were found in all zones. SNK tests between the caged and cleared treatments showed no significant differences (Fig. 2, Table 3b). Thus, where the settlement surface was protected from sweeping, recruitment was high despite the presence of an overlying canopy.

Comparison of recruitment between zones showed that the *F. spiralis* zone had significantly lower levels of recruitment than the two lower shore heights despite having the highest level of settlement (Fig. 2, Table 3b). Recruitment levels in the *Ascophyllum* and *Fucus serratus* zones were similar, although the reduction in recruitment to the control treatment was far more pronounced in the *F. serratus* zone. At the end of the settlement season, recruitment to the control treatment under the *Ascophyllum* canopy was 8 times greater than under the *F. serratus* canopy.

3.1.3. Post-settlement mortality

The effect of the canopy on post-settlement mortality was determined by sampling settlement tiles over the three month period following the end of the settlement season. To avoid confounding of density-dependent effects with canopy effects a comparison was made between tiles bearing initially similar barnacle densities. Fouling of settlement tiles by ephemeral algae prevented determination of mortality in cleared plots of the *F. serratus* zone.

Instantaneous mortality rates for each individual replicate were calculated by determining the regression coefficients of the natural log of percentage survival against time (Fig. 3). The effect of the fucoid canopy was the same at both shore levels investigated, with mortality significantly lower beneath the fucoid canopy than in cleared areas (Table 4, Fig. 3). Mortality was also significantly higher in the high shore *F. spiralis* zone than in the mid shore *Ascophyllum* zone.

Increased mortality in areas cleared of canopy resulted in a convergence of barnacle densities between the control and cleared treatments. This was more pronounced in the high shore *F. spiralis* zone. At the final sampling date in October there was no difference between treatments (ANOVA, $P > 0.25$).

3.1.4. Recruitment onto natural substrata

No recruitment to natural substrata occurred beneath the canopy of either *F. serratus* or *Ascophyllum* (Fig. 4). In the cleared areas of these zones, recruitment occurred, but at over an order of magnitude less than on settlement tiles. In the *F. spiralis* zone, where adult barnacles were relatively common, recruitment to natural substrata was not as depressed as lower on the shore. However, in both treatments recruitment was over two times higher on settlement tiles, probably reflecting the greater cover of adult conspecifics compared to the natural substrata.

3.2. Experiment 2: Castletown 1994

On all three sampling dates, there was no cyprid settlement to tiles in the *F. spiralis* zone. Thus conclusions regarding treatment effects can only be made for the mid and low shore. This observation may have been a result of sampling occurring during a period of neap tides during which inundation of the high shore was minimal.

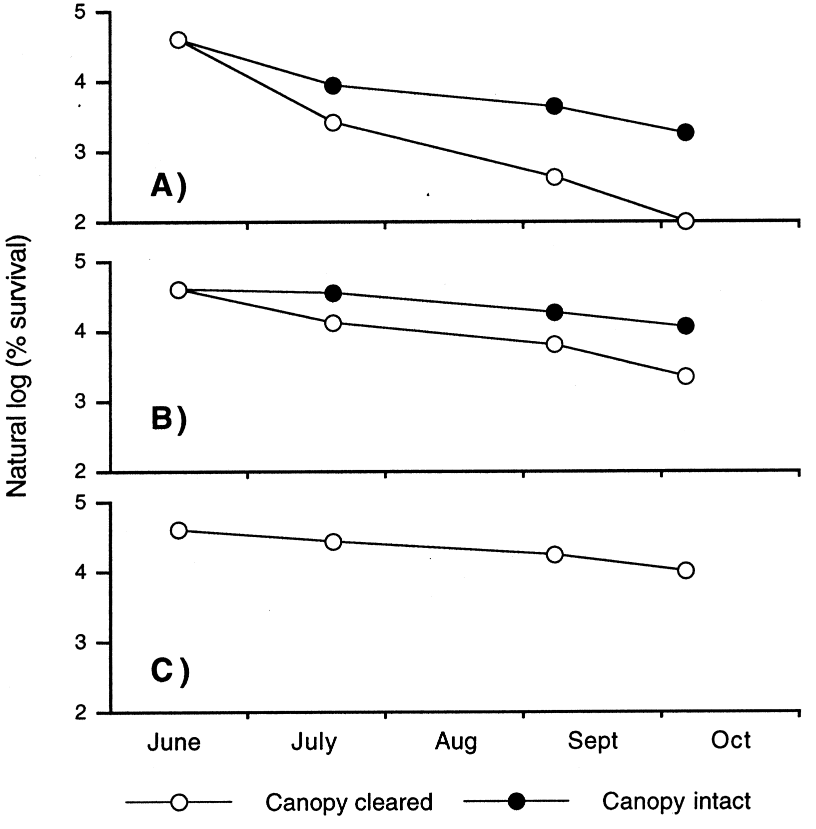

Fig. 3. Experiment 1: Natural log of percent survival of *S. balanoides* spat over the 4 month period following the end of the settlement season. (A) High shore *F. spiralis* zone. (B) Mid shore *Ascophyllum* zone. (C) Low shore *F. serratus* zone.

Data for the mid and low shore are only presented for the first sampling date although exactly the same trend was shown at all three dates. The effect of the three canopy treatments clearly differed between the *F. serratus* and *Ascophyllum* zones; there was a highly significant interaction between treatment and shore height (Table 5, Fig. 5). In the *F. serratus* zone settlement in the two cleared treatments was consistently higher than in

Table 4
Two way ANOVA of regression coefficients testing for the effect of fucoid canopy cover and shore height on the percent survival of new *S. balanoides* recruits

Source	df	MS	*F*	*P*
Canopy	1	5.43×10^{-4}	18.22	< 0.0002
Shore height	1	6.37×10^{-4}	21.35	< 0.0001
Canopy × Height	1	6.11×10^{-5}	2.05	> 0.16
Residual	28	2.98×10^{-5}		

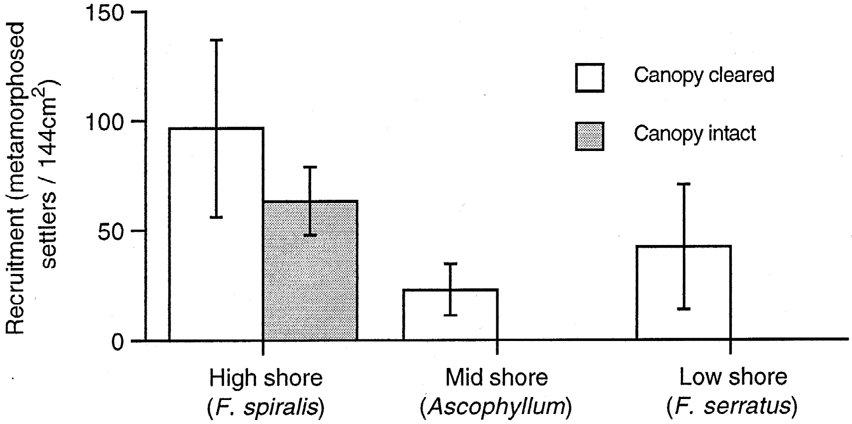

Fig. 4. Experiment 1: Mean number (± SE) of metamorphosed individuals of *S. balanoides* present on natural substrata on 1st June 1993.

the canopy treatment. Thus, despite being protected from the sweeping effects of *F. serratus* fronds, settlement beneath the canopy was apparently limited. This was clearly not an artefact of the cages since settlement in cleared areas was the same irrespective of the presence or absence of a cage. SNK tests confirmed these conclusions; tiles beneath the canopy showed significantly lower settlement than those in cleared areas (Table 5). In contrast, settlement in the *Ascophyllum* zone was similar between all three treatments (Fig. 5, Table 5).

Table 5
Two way ANOVA and SNK multiple comparisons of square root transformed data testing for the effect of shore height and canopy treatments on the settlement of *S. balanoides* cyprids on 16th May 1997 in experiment 2

Source	df	MS	*F*	*P*		
Canopy treatment	2	62.10	5.94	<0.0067		
Shore height	1	1003.94	96.05	<0.0001		
Treatment × Height	2	212.16	20.30	<0.0001		
Residual	30	10.45				
SNK multiple comparisons of interaction						
	Ascophyllum	*F. serratus*	Cleared (caged)	Cleared (no cage)	Canopy	
Cleared (caged) v cleared (no cage)	NS	NS	*F. serratus* v *Ascophyllum*	S	S	NS
Cleared (caged) v canopy intact	NS	S				
Cleared (no cage) v canopy intact	NS	S				

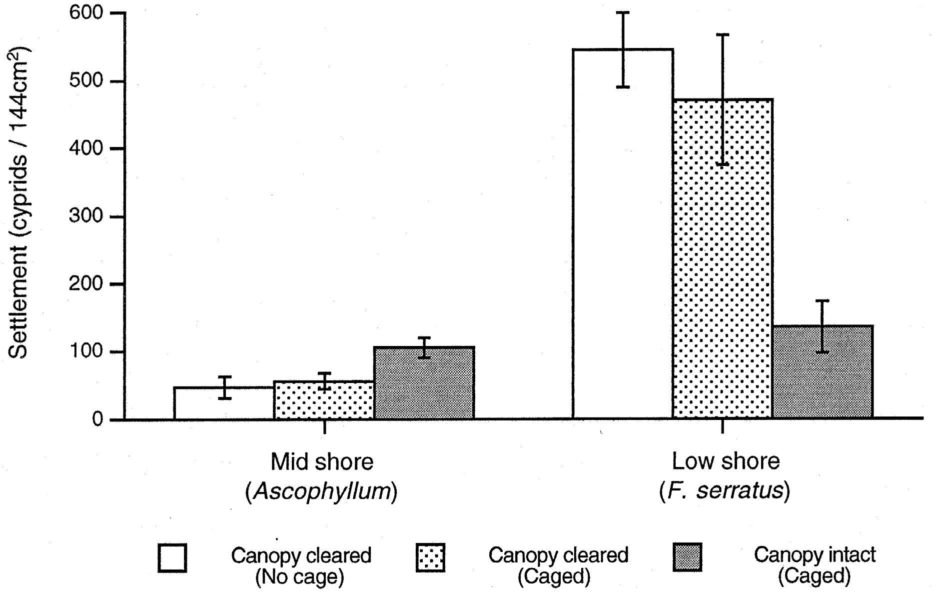

Fig. 5. Experiment 2: Mean number (± SE) of *S. balanoides* cyprids present on settlement tiles on one sampling date (16.5.97).

3.3. Experiment 3: Port Erin 1994

3.3.1. Experiment A: Sweeping effects on newly settled cyprids

Newly settled cyprids of *S. balanoides* were extremely vulnerable to sweeping by *F. serratus* plants. Only 3% of the cyprids originally present on 'smooth' tiles survived over a single high water period when transplanted beneath the canopy. Survival was significantly higher (32%) when cyprids settled within a mosaic of adult barnacles (One way ANOVA: $F_{(2,30)} = 276.37$, $P < 0.0001$). However, whether on 'rough' or 'smooth' tiles survival beneath the canopy was significantly lower than in cleared areas where over 90% of individuals survived (SNK: $P < 0.05$).

3.3.2. Experiment B: Comparison of sweeping effects on newly settled cyprids and newly metamorphosed spat.

The survival of newly metamorphosed spat over one high water period showed very little difference with that of newly settled cyprids both beneath the canopy and in cleared areas (Fig. 6). Survival of both these stages was less than 18% beneath the canopy. It thus appears that metamorphosis of cyprids into spat does not confer any additional resistance to the sweeping of *F. serratus* fronds. Two way ANOVA on arc-sin transformed data shows a highly significant effect of the canopy ($F_{(1,21)} = 116.9$, $P < 0.0001$) but no effect of developmental stage ($F_{(1,21)} = 0.008$, $P > 0.9$) on percentage survival.

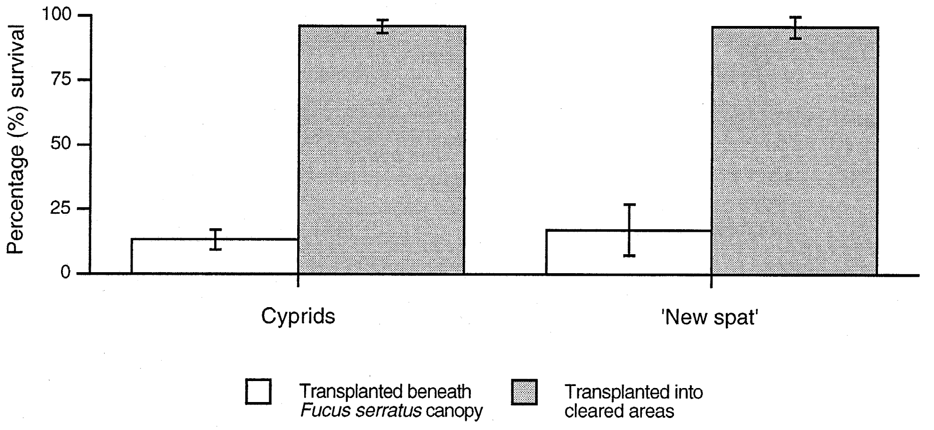

Fig. 6. Experiment 3B: Mean percentage survival (± SE) of *S. balanoides* cyprids and newly metamorphosed spat over one high water period on June 10th 1994 in the low shore *F. serratus* zone.

3.3.3. Experiment C: Comparison of sweeping effects on newly settled cyprids, newly metamorphosed spat and six day old spat.

Although metamorphosis of cyprids to spat did not increase survival, an increase in age of spat appeared to do so. Six-day-old spat showed 51% survival over one high water period under the *Fucus* canopy, significantly greater than for cyprids (7% survival) and newly metamorphosed spat (4% survival) (One way ANOVA: $F_{(2,12)} = 8.92$, $P < 0.005$; SNK: $P < 0.05$).

Observations made at the time showed that the sea state varied quite considerably between experiments 3A, B and C. Mean wind speed and direction were calculated using data from Ronaldsway Meteorological Office for the 12 h and 24 h periods before the time of high water at which the sweeping event of each of the three experiments took place. The predicted sea state at the experimental site was highest in experiment A, lowest in experiment C and intermediate in experiment B. There was no relationship between sea state and percentage survival of cyprids beneath the *F. serratus* canopy in the three separate experiments.

4. Discussion

Macroalgal canopies form dense stands on a variety of rocky shores, but particularly those sheltered from wave action. Previous work on such shores has suggested that canopy algae can have both positive and negative effects on barnacle recruitment (Hawkins, 1983). The magnitude of these effects and the balance between them will depend upon the physical characteristics of the canopy species and the vertical height on the shore. Although it is not possible to separate the effect of canopy type from vertical height, a consideration of the nature of the three canopy species will aid interpretation of results. All three canopy species differ significantly in their form. *Fucus serratus* is a bushy, bladderless plant which forms a dense, low cover over the substratum when submerged. In contrast, *Ascophyllum nodosum* has abundant bladders and stands erect in the water column, leaving large areas between the plants free from algal influence. Bladders in *Ascophyllum* probably reduce the disturbance at the water-rock interface caused by the sweeping of algal fronds (Bennell, 1981). The bladderless *Fucus spiralis* forms a low canopy which lacks the size and density of the *F. serratus* stands. At our study site, all three species formed a complete cover over the substrate when emersed, and hence their ability to reduce desiccation during low water periods was probably comparable. The importance of desiccation however will obviously increase with height on the shore.

On sheltered shores, dense stands of canopy algae may form a barrier to the water-borne movement of plant and animal propagules and thus influence the establishment of benthic communities (Hatton, 1938; Lewis and Bowman, 1975; Deysher and Norton, 1982). For example, the presence of several algal canopy species has been shown to inhibit colonisation of *Sargassum muticum* (Deysher and Norton, 1982). It was proposed that the algae formed a physical barrier between settling germlings and the substratum. This phenomenon has also been suggested to inhibit the establishment of limpets on sheltered shores, although no tests of this hypothesis have been made (Fischer-Piette, 1948; Lewis and Bowman, 1975). Subtidal kelp forests have a significant impact on fluid and particulate transport and can inhibit transport of suspended particles from the overlying water column to the bottom (Eckman et al., 1989). Examination of the influence of such flow effects on recruitment of a range of benthic invertebrates gave mixed results, but showed that the recruitment of some species (e.g. *Membranipora membranacea*) can be reduced by the impact of kelps on the flow regime (Duggins et al., 1990). Gaines and Roughgarden (1987) showed that variation in the area covered by subtidal kelp forests on the coast of California was a major cause of variation in barnacle recruitment to the intertidal zone. However, this recruitment variation was thought to be a result of the indirect effect of larval predation by juvenile rockfish living within the kelp forest, rather than any direct effect of canopy on water flow or larval transport.

Despite the aforementioned work, no investigation has directly attempted to investigate whether macroalgal canopies may form some kind of barrier to larvae and propagules in the intertidal zone. The potential effect of the canopy as a barrier is always confounded with other effects such as sweeping. A barrier may act in a number of ways, by forming a physical barrier to larval movement, by reducing water circulation and mixing and by creating a 'behavioural barrier'. Given the complex behaviour patterns and discriminatory processes seen in many planktonic larvae it is feasible that chemical or physical cues from canopy algae may discourage larvae from seeking the substratum. Whatever the mechanism, if a canopy creates a barrier then the concentration of larvae at the substratum will be reduced and settlement and recruitment will be limited.

The most direct method of investigating a potential barrier effect would be to sample the planktonic supply of larvae to the substratum in the presence and absence of the canopy. This presents many logistical difficulties and consequently we used a more indirect approach and analysed settlement and recruitment under different experimental treatments. Any reduction in settlement and recruitment to tiles placed beneath the canopy, which were protected from the sweeping of algal fronds, was assumed to be the result of the canopy acting as some form of barrier. In the low shore *F. serratus* zone, levels of settlement in experiments 1 and 2 indicate that this alga forms a barrier to cyprid movement, limiting their access to the substratum. Settlement on caged tiles under the canopy was consistently lower than to tiles in cleared areas. In contrast, we obtained mixed results in the *Ascophyllum* zone. In experiment 2 results indicated this species does not inhibit cyprid movement. These results are consistent with the physical characteristics of these two plants. When emersed both appear to form a continuous cover over the substratum, but when submerged the erect nature of *Ascophyllum* presents little in the way of a barrier in comparison to the bushy *F. serratus*.

As well as providing evidence of a barrier effect, our results confirm the importance of sweeping in determining the abundance of settled barnacles. At all three shore levels, there was a clear inhibitory effect of sweeping, with a significant difference between caged and unprotected tiles beneath the canopy. This difference was greatest in the *F. serratus* zone. Again, this result is consistent with the physical nature of this species; *F. serratus* has no bladders and relatively heavy fronds and is thus a more effective 'sweeper' than the bladdered *Ascophyllum* and much lighter *F. spiralis*.

A number of studies have quantified levels of early post-settlement mortality in barnacles on surfaces free of algae (e.g. Connell, 1961; Wethey, 1985; Gosselin and Qian, 1996). Wethey (1985) observed levels of mortality of newly settled *Semibalanus balanoides* over a five day period to be as high as 90% and 60% on the high and mid shore respectively. Connell (1961) showed that approximately 20% of attached cyprids died before they metamorphosed, while Gosselin and Qian (1996) showed that mortality over the first day after settlement was as high as 38% in *Balanus glandula*. These levels are very low in comparison to the mortality of cyprids and newly metamorphosed spat of *S. balanoides* observed beneath a canopy of *F. serratus*. By monitoring marked individuals, mortality levels of between 82 and 97% over just one high water period were recorded, illustrating the large effect of algal sweeping on recruitment. The presence of adult barnacles significantly increased survival beneath a canopy. Cyprids that had settled within a mosaic of adults were roughly ten times more likely to survive over a high water period than were those on surfaces where adults had been cleared. This effect appears comparable to the protection from limpet grazing provided by adult barnacles (Hawkins, 1983; Miller, 1989). Thus, gregarious settlement in barnacles not only acts as a means of preventing settlement on substratum which is unsuitable, because for example it is above the natural tolerable limits of the species (Hui and Moyse, 1987), but may also reduce early post-settlement mortality by physical dislodgement.

The sweeping action of algal fronds over the substratum is obviously a major source of mortality to settling cyprids. This developmental stage appears intrinsically fragile and prone to mechanical damage whether from waves, sweeping algae or gastropod grazing. Once metamorphosed, barnacles radically change their appearance and it is tempting to assume that their resistance to damage is dramatically increased. At settlement, cyprids permanently attach to the substratum using a proteinaceous secretion, the cyprid cement (Walker, 1971). Additional cement is laid down within one day after settlement and gradually increases in area over time (Yule and Walker, 1984). Our results show that this addition of 'juvenile cement' and the radical change in form at metamorphosis did not result in an increase in the resistance of newly metamorphosed individuals to sweeping. However, a significant increase in resistance was found in six day old spat, indicating that resistance to dislodgment probably increases progressively as shell plates strengthen with calcification and juvenile cement is laid down (Yule and Walker, 1984). These results are consistent with those of Wethey (1985), who found that mortality rates of cyprids and uncalcified metamorphs (1 day old) on substrata free from algae were indistinguishable and that the majority of mortality occurred during the first five days after settlement.

Over the settlement period, canopy algae clearly had a negative effect on recruitment of barnacles. It is only after becoming established on the rock surface and reaching a size at which sweeping was no longer a danger that canopy algae had a positive influence through the moderation of microclimate. Dayton (1971) and Hawkins (1983) both showed that canopy algae can enhance survival of newly settled barnacles on the high shore. We found a positive effect of the canopy on the survival of established *S. balanoides* in the *F. spiralis* and *Ascophyllum* zones in the three months following the end of the settlement season. This effect was strongest in the high shore where desiccation is obviously higher. Fouling of settlement tiles by ephemeral algae prevented an evaluation of the canopy effect in the *F. serratus* zone.

Enhanced survival under the canopy probably explains the apparently contradictory results provided by settlement and recruitment data in experiment 1. At all shore heights recruitment (number of metamorphosed individuals) to caged tiles beneath the canopy was equivalent to tiles in cleared areas. In contrast, settlement (number of cyprids) was significantly lower in the caged treatment. These conflicting results may be explained by considering the effect of the canopy on post-settlement survival. Despite lower settlement beneath the canopy, enhanced survival may result in equivalent levels of recruitment in both canopy and cleared treatments. These results confirm the importance of high sampling frequency if an accurate measure of settlement is to be obtained (Minchinton and Scheibling, 1993).

Lower levels of post-settlement mortality resulted in the density of recruits on tiles beneath the canopy converging on those in cleared areas in both the *F. spiralis* and *Ascophyllum* zones. This observation, whilst demonstrating that canopy algae can have a positive as well as a negative effect on recruitment of barnacles to the adult population does not necessarily lead to the conclusion that canopies have little overall effect on recruitment to sheltered shores. The significance of a settlement stimulus must be noted in evaluating the long term effects of canopy algae. In the absence of a canopy, some settlement occurred on natural substrata lacking a stimulus. However, where the canopy was present no settlement at all occurred in the *Ascophyllum* and *F. serratus* zones. Under natural conditions in the mid and low shore (where adult barnacles are rare) it is likely that the inhibitory effect of the canopy on settlement has a profound influence on the development of barnacle populations. On the high shore, barnacle populations are common and although the *F. spiralis* canopy does inhibit settlement the enhancement of post-settlement survival results in a neutral or positive effect of the canopy on barnacle populations.

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