J. Mar. Biol. Ass. U.K. (1999), **79**, 341–349
Printed in the United Kingdom

Interactions between canopy forming algae in the eulittoral zone of sheltered rocky shores on the Isle of Man

Stuart R. Jenkins, Trevor A. Norton and Stephen J. Hawkins*

Port Erin Marine Laboratory, University of Liverpool, Port Erin, Isle of Man, IM9 6JA.
*Division of Biodiversity and Ecology, University of Southampton, Biomedical Sciences Building, Bassett Crescent East, Southampton, SO16 7PX

The distribution and abundance of *Ascophyllum nodosum*, *Fucus serratus* and *F. vesiculosus* were described at four sheltered, rocky shores in the south of the Isle of Man. Canopy removal experiments were performed at mid tide level of one sheltered, canopy dominated shore to investigate the interactions between the dominant canopy alga, *Ascophyllum nodosum* and the competitively inferior canopy species of *Fucus serratus* and *F. vesiculosus*. *Ascophyllum* was removed from replicated plots, 2×2 m in size, in both winter and summer; the early growth and survival of fucoids in the presence and absence of the *Ascophyllum* canopy were monitored and the eventual development of a new canopy described. Juveniles of *F. serratus* originally present beneath the undisturbed canopy of *Ascophyllum* died following canopy removal but new recruitment resulted in some canopy development, principally in the winter experiment. *Fucus vesiculosus*, despite being completely excluded from the *Ascophyllum* zone of all four shores described, dominated the canopy removal plots of both winter and summer experiments. The *Ascophyllum* canopy did not recover over a five year period of observation, although a considerable increase in the abundance of *Ascophyllum* juveniles occurred.

INTRODUCTION

Sheltered rocky shores of north-west Europe are dominated by canopy forming fucoid algae. In very sheltered areas a continuous cover of canopy from the high shore to the sublittoral zone may occur. A dominant feature of such shores is the often extensive mid shore zone of *Ascophyllum nodosum* (L.) Le Jolis which is very stable over time (Lewis, 1964).

David (1943) considered that in the mid shore of sheltered areas the three fucoid species, *A. nodosum*, *Fucus vesiculosus* L. and *Fucus serratus* L. compete for space. The abundance and zonation of these three species shows great variability (Lewis, 1964), although some general patterns are consistent. *Fucus serratus* generally forms a distinct zone low on the shore between the mid shore *Ascophyllum* and the laminarians of the sublittoral fringe. The vertical position of *F. vesiculosus* may vary according to the degree of shelter, either forming a mixed population with *Ascophyllum* (Lewis, 1964; Hawkins et al., 1992) or in more sheltered areas being restricted to a narrow fringe at the top of the *Ascophyllum* belt. Occasionally a belt beneath *Ascophyllum* can occur (Lewis, 1964). On Manx sheltered shores the mid shore is dominated by *Ascophyllum*. Within this apparently monospecific canopy, *F. serratus* is abundant especially in the low and mid parts of the *Ascophyllum* zone. *Fucus vesiculosus* is scarce and restricted to the upper part of the zone.

The community ecology of the *Ascophyllum* zone of sheltered sites has been relatively neglected. A number of studies have investigated the potential of *Ascophyllum* for regrowth or recolonization in harvested or experimentally denuded areas, both in Europe (Printz, 1956) and North America (Keser et al., 1981; Keser & Larson, 1984; Sharp, 1986). Studies examining the interaction between *Ascophyllum* and other canopy species are rare and have been mainly concerned with understanding the pattern of vertical zonation (e.g. Hawkins & Hartnoll, 1985). Many authors have remarked upon the surprisingly low levels of *Ascophyllum* juveniles which recruit into mature stands (Oltmanns, 1889; David, 1943; Knight & Parke, 1950; Printz, 1956; Baardseth, 1970; Vadas et al., 1990), although a recent study has reported densities as high as 46 juveniles m^{-2} in the upper part of the *Ascophyllum* zone (Aberg & Pavia, 1997). However, recruitment of *Ascophyllum* is certainly low in relation to the large investment placed into reproductive biomass (Josselyn & Mathieson, 1978; Cousens, 1986; Aberg, 1996) and it seems survival and growth of established plants is more important for population growth than sexual reproduction (Aberg, 1992). These factors combined with the slow growth rate of *Ascophyllum* (Schonbeck & Norton, 1980) make investigations into competitive interactions in this zone difficult.

Competition among marine macroalgae has been demonstrated or suggested to be important in determining the distribution and abundance of species in both intertidal (Dayton, 1975; Hawkins & Hartnoll, 1985; Chapman, 1990), and subtidal communities (Dayton et al., 1984; Reed & Foster, 1984). Although *Ascophyllum* is clearly dominant on sheltered shores, it grows slowly compared to *Fucus* species with which it competes (Schonbeck & Norton, 1980). Combined with low recruitment, recolonization of disturbed areas is very slow. The aim of this work was to investigate the interactions between *Ascophyllum* and subdominant *Fucus* species, particularly their juvenile stages, in order to gain an insight into the causes of some of the variability in fucoid distribution in sheltered and semi-sheltered sites. *Ascophyllum* was experimentally removed to test the hypothesis that this canopy alga limits the recruitment and growth of *Fucus* juveniles and in so doing inhibits the development of *F. serratus* and *F. vesiculosus* canopies in the mid shore of sheltered sites. *Fucus vesiculosus* and *F. serratus* have distinctly different periods of reproduction on the Isle of Man (Creed, 1993) and it was hypothesized that the timing of canopy removal would determine which species of *Fucus* colonized the mid shore. Thus experiments were carried out with both winter and summer start dates. The ability of *F. serratus*, a predominantly low shore species, to compete at mid shore level was tested by examining the growth rates of juveniles in undisturbed areas of the *F. serratus* and *Ascophyllum* zones. It was hypothesized that growth rate would decrease with shore height.

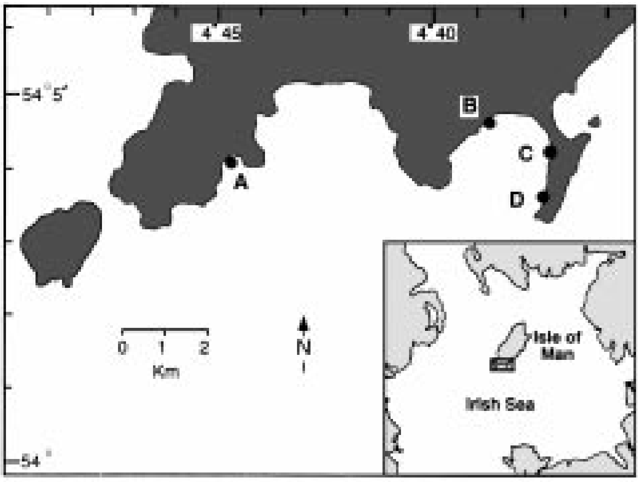

Figure 1. Location of four sheltered sites (A–D) in the south of the Isle of Man used in August 1994 to describe the distribution of fucoid species in the mid shore. Inset map shows the position of the Isle of Man in the Irish Sea; the black rectangle depicts the area covered by the main map.

MATERIALS AND METHODS

Distribution of fucoids on Manx sheltered shores

Descriptive sampling of the *Ascophyllum* zone took place in August 1994 at four sheltered shores in the south of the Isle of Man, at Perwick Bay (site A), at the northern edge of Castletown Bay (site B) and on the Langness Peninsula (sites C and D) (Figure 1). All shores were dominated by *Ascophyllum* at mid shore level. The abundance of *Ascophyllum*, *Fucus serratus*, and *F. vesiculosus* was estimated at each of three shore heights (high, mid and low) throughout the *Ascophyllum* zone. Eighteen $0.25\,m^2$ quadrats, subdivided into 25 squares were placed at random along a single horizontal transect at each shore height and percentage cover of each canopy species estimated. Thus for each of the four sites, 54 quadrats were sampled and the whole extent of the *Ascophyllum* zone was covered.

Experimental clearance of Ascophyllum nodosum

The effect of the *Ascophyllum* canopy on the recruitment, growth and canopy development of competing fucoids was examined by undertaking canopy clearances in two seasons. A single treatment (removal of *Ascophyllum* canopy) and control (no removal) were used, treatment and control each being replicated three times. The experiment was run twice, once with a winter, and once with a summer start date. The analysis consisted of two main factors, canopy and season, both fixed and orthogonal to each other. The lack of temporal replication of the experiment within each season means the test for differences between winter and summer is confounded (Underwood, 1997). Thus conclusions based on a significant effect of the factor season should be treated with caution. Experimental plots were sampled at intervals over three years to investigate the pattern of recruitment and canopy development. Analysis of variance was performed on data obtained a fixed period of time from each of the winter and summer start dates.

A site for experimental work was selected on the west side of the Langness Peninsula on the Isle of Man, the mid shore of which is dominated between 2.7 and 4.8 m above lowest astronomical tide (LAT) by an extensive bed of *Ascophyllum*. In November 1991 six plots were chosen within the middle of the *Ascophyllum* zone between 3.3 and 4.3 m above LAT. These were all positioned in areas of smooth, gently sloping topography with a dense cover of *Ascophyllum*. Rockpools and irregularities in inclination were avoided. The plots were spread throughout the experimental site such that a minimum of 5 m separated any two plots. In this way replicates were positioned so that they were independent of each other and sufficient space was left between plots to enable a subsequent experiment to be established the following summer. This took place in June 1992.

At each plot an area 2×2 m square was measured. Holes were drilled into the rock at the four corners of each square using a petrol driven Ryobi™ hammer action drill. Plastic rawlplugs were used to enable steel ring-bolts to be securely screwed into each hole. To aid the location and identification of plots beneath the dense *Ascophyllum* canopy, a 40 cm length of orange and yellow fluorescent 'Twinglow' tape was numbered and tied to each ring-bolt.

The control and treatment described above were assigned at random to the six plots. Before any manipulation took place, each plot was sampled (see below).

The *Ascophyllum* canopy was removed using a wide bolster chisel. Every adult plant (including those of *F. serratus*) within the 2×2 m area was removed, including as much of the holdfast as possible. Individuals less than 5 cm in length of both *Ascophyllum* and of *F. serratus* were not removed. In order that the area could be considered free from the influence of the *Ascophyllum* canopy, individual plants surrounding the plot which could overhang onto its surface were cropped using a pair of garden shears. Thus the three plots in which the *Ascophyllum* canopy was removed consisted of a central 2×2 m area in which all traces of adult plants were removed, surrounded by a zone up to 1.5 m wide in which individuals had been reduced in size.

Sampling

Plots were sampled at approximately six week intervals over the first two years of study and thereafter less frequently up to three years. Observations were made after five years to determine the extent to which *Ascophyllum* had recovered. At the regular sampling dates a 0.5×0.5 m quadrat subdivided into 25 equal squares was placed at random, four times within each plot. The number of fucoid juveniles in each quadrat was counted and the percentage cover of the different species of canopy algae estimated. Overlapping species meant that total cover could be greater than 100%. The four subsamples taken from within each plot were used to calculate a mean value for each replicate. Subsamples were used in this way in order to increase the precision of estimation of each experimental unit (Hurlbert, 1984).

Fucoid juveniles were considered as individuals less than 5 cm in length, excluding plants that by breakage had decreased in size. The very slow growth rate of *Ascophyllum* means a 5 cm long plant is probably several years old. Thus the term juvenile is used in the sense of size and non reproductive status as opposed to age. The removal of *Ascophyllum* holdfast tissue at the start of the experiment ensured that juveniles sampled were not formed from regrowth of partly removed plants.

Growth rate and survival of Fucus serratus *juveniles*

The effect of the *Ascophyllum* canopy on the growth rate and survival of fucoid juveniles naturally present in the *Ascophyllum* zone was examined in the clearances and controls of the experiment described above. Initially both *F. serratus* and *Ascophyllum* juveniles were used, but the very low density of *Ascophyllum* juveniles prevented a meaningful level of replication for this species. In both the winter and summer experiments six areas measuring 0.5×0.5 m were selected; three were within plots cleared of canopy and three within control plots where the canopy was left intact. Areas were chosen with a uniform algal turf and a high density of fucoid juveniles.

The corners of each 0.5×0.5 m area were marked by small stainless steel screws, secured in drilled holes by plastic rawlplugs. By positioning the 0.5×0.5 m quadrat over the locator screws, the exact position of all juveniles (plants <5 cm tall) was mapped in relation to the quadrat grid. Although at the beginning of the experiment juveniles of *F. serratus* and *F. vesiculosus* could not be distinguished, experience subsequently allowed identification. It was found that all juveniles beneath the intact *Ascophyllum* canopy and therefore all those monitored were *F. serratus*. The length of these individuals from holdfast to frond tip was then measured. At approximately six weekly intervals, individuals were relocated using the mapping system and re-measured. Notes were made on their condition. In the summer experiment, high mortality in cleared plots resulted in insufficient numbers of juveniles to be able to effectively estimate growth rate. Thus data on growth were only obtained for the winter experiment.

Relative growth rate (RGR) (Evans, 1972) was used to measure change in size over time. The RGR per day for each juvenile was calculated as follows:

$$\mathrm{RGR} = \frac{\log_e l_2 - \log_e l_1}{(t_2 - t_1)} \quad (1)$$

where l_1 and l_2 are the total lengths (cm) of fucoid juveniles at the beginning and end of a period from t_1 to t_2 days.

Comparison of the growth rate of Fucus serratus *juveniles between the* Ascophyllum *and* F. serratus *zones*

The relative abundance of *F. serratus* juveniles in the *Ascophyllum* zone enables a comparison of their growth rate between the mid shore where adult plants are relatively rare and the low shore where adult *F. serratus* can form a 100% cover. Three positions between 4 and 20 m apart within the middle of both the *F. serratus* and *Ascophyllum* zones were selected where the juveniles were common and the canopies formed an uninterrupted cover. Between 15 and 25 juveniles in the size range 20–50 mm were individually tagged at each of the six positions. The presence of any grazing damage was assessed and recorded.

Tags were made from lengths of 'lacing cord' (RS Components) dipped in white enamel paint to make them more visible. Numbered micromarkers were glued onto small aluminium rings (2 mm diameter) which were then passed over the two ends of a short length of lacing cord to produce a loop. The loop could then be placed over a juvenile plant and positioned just above the holdfast. The ring was then slid along the cord to shorten the loop to such an extent that the tag could slide up and down the lower portion of the plant, but not slide off. The ring was crushed using a pair of pliers to hold it firmly in place.

All tagged plants were measured to the nearest millimetre approximately every 3–4 weeks. This method of tagging allowed quick and easy identification of individual plants. However, unlike the mapping system used to monitor growth rates of juveniles in the section above, this method did not allow estimation of the mortality rate. The inability to relocate a tagged plant could not be assumed to mean death of that plant since loss of the tag was equally likely.

Analysis of data was undertaken using the statistical package SuperANOVA™. Prior to analysis, data were tested for homogeneity of variance using Cochran's test. Where appropriate multiple comparisons of significant factors were made using Student–Newman–Keuls (SNK) tests.

RESULTS

Distribution of fucoids on Manx sheltered shores

The *Ascophyllum* zone occupied roughly similar levels on all four shores sampled with the maximum range occurring at site D, between 2.5 and 5.0 m above LAT. *Ascophyllum* formed a canopy cover of almost 100% (Figure 2) with occasional patches of *Fucus serratus* being visible especially toward the lower part of the zone. Detailed quantitative examination revealed cover of *F. serratus* averaged over the whole zone ranged between 25% at site A and 6% at site B, the majority occurring as a subcanopy, obscured and overshadowed by the much

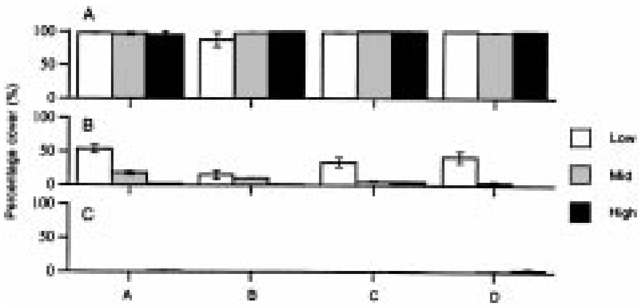

Figure 2. Cover of fucoid canopy at three tidal heights within the *Ascophyllum* zone at four sheltered shores (A–D) in the south of the Isle of Man: (A) *Ascophyllum*; (B) *Fucus serratus*; (C) *Fucus vesiculosus*. Error bars: ±1 SE.

Table 1. *ANOVA of fucoid canopy species distribution.*

Source	df	Mean square	*F*-value	*P*-value	*F*-ratio vs
Shore	3	301.4	1.80	0.1485	Error
Height on shore	2	2486.1	11.33	0.0092	Sh×H
Species	2	195614.9	1868.05	0.0001	Sh×Sp
Shore × Height	6	219.4	1.31	0.2539	Error
Shore × Species	6	104.7	0.63	0.7093	Error
Height × Species	4	3587.3	30.18	0.0001	Sh×H×Sp
Shore × Height × Species	12	118.9	0.71	0.7398	Error
Error	180	167.3			

larger plants of *Ascophyllum*. *Fucus vesiculosus* was almost completely absent from the *Ascophyllum* zone at all sites (Figure 2). Analysis of the distribution of the three canopy species between shores and shore heights was undertaken using three way ANOVA, with species, height

Table 2. *ANOVA of fucoid juvenile density.*

Source	df	Mean square	*F*-value	*P*-value
A. *Ascophyllum* juveniles.				
Canopy	1	567.57	22.16	0.0015
Season	1	44.59	1.74	0.2235
Canopy×Season	1	2.86	0.11	0.7470
Error	8	25.61		
B. *Fucus* juveniles.				
Canopy	1	859.46	24.34	0.0011
Season	1	28.77	0.82	0.3931
Canopy×Season	1	14.91	0.42	0.5339
Error	8	35.31		

Data for both analyses square root transformed to meet the assumption of homogeneity of variance.

on shore and shore as factors all orthogonal to each other. The factors species and height were considered fixed and shore random. In order to ensure independence between samples, six replicate quadrats were used for each of the three species from the 18 quadrats available at each shore height. Analysis revealed a significant interaction between height and species (Table 1). Examination of figure 2 shows this result is clearly a consequence of the difference in percentage cover of *F. serratus* between shore heights. Cover increased from high to low levels at all shores examined. The other two species, *Ascophyllum* and *F. vesiculosus* showed no change in cover with shore height.

Fucoid juvenile recruitment

Removal of the *Ascophyllum* canopy resulted in a dramatic increase in the density of *Ascophyllum* juveniles. Fourteen months after canopy removal densities of 173 and 363 juveniles m^{-2} were found in the winter and

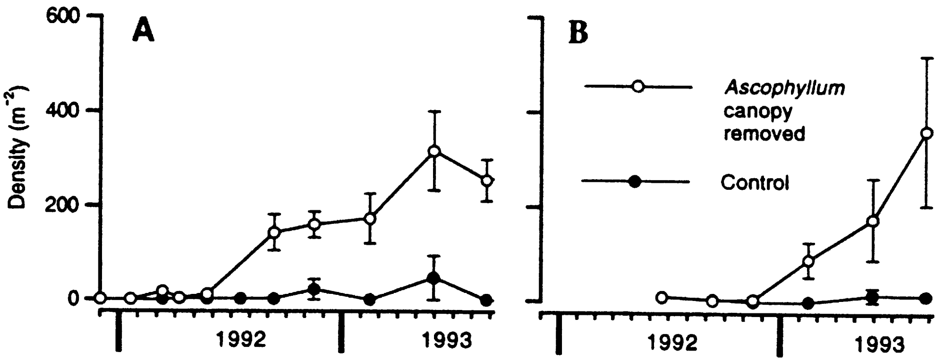

Figure 3. Change in density of *Ascophyllum* juveniles following removal of the *Ascophyllum* canopy: (A) winter experiment; (B) summer experiment. Error bars: ±1 SE.

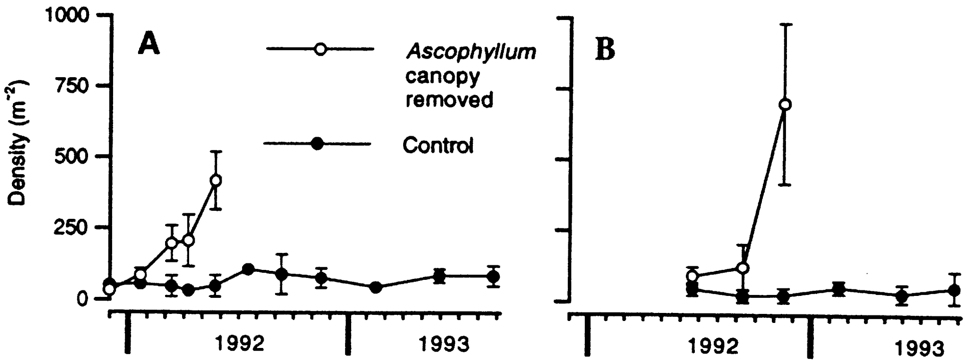

Figure 4. Change in density of *Fucus* juveniles following removal of the *Ascophyllum* canopy: (A) winter experiment; (B) summer experiment. Error bars: ±1 SE.

https://doi.org/10.1017/S0025315498000381 Published online by Cambridge University Press

Table 3. *ANOVA of fucoid canopy development.*

Source	df	Mean square	*F*-value	*P*-value
A. *Fucus vesiculosus*.				
Canopy	1	17941.33	225.44	0.0001
Season	1	85.33	1.07	0.3307
Canopy × Season	1	85.33	1.07	0.3307
Error	8	79.58		
B. *Fucus serratus*.				
Canopy	1	266.02	1.16	0.3124
Season	1	117.19	0.51	0.4946
Canopy × Season	1	28.52	0.13	0.7332
Error	8	228.85		

summer experiments respectively (Figure 3). The effect of canopy manipulation was highly significant, while no effect of season was found (Table 2A). *Fucus* juveniles also showed a sharp increase in density in areas cleared of canopy (Figure 4) although in contrast to juveniles of *Ascophyllum*, this occurred immediately following experimental manipulation. Densities of *Fucus* juveniles in canopy cleared areas were such that sampling was not continued beyond six months due to difficulty in counting the densely packed plants. The *Fucus* juveniles sampled in canopy cleared areas were a mixture of *F. serratus* and *F. vesiculosus* juveniles. The relative densities of these two species could not be determined owing to identification difficulties but in all plots where the canopy was left intact only *F. serratus* juveniles were present. The effect of canopy clearance in determining density of *Fucus* juveniles was highly significant and again no effect of season was found (Table 2B).

Fucoid canopy development

Regrowth of the *Ascophyllum* canopy, following its removal did not occur during the experimental period of three years with no *Ascophyllum* canopy cover in cleared plots after this period of time. New recruits had reached only approximately 5 cm in length while a few individuals, probably previously established juveniles had reached a maximum size of 10 cm. In contrast, canopies of *F. vesiculosus* developed rapidly after *Ascophyllum* removal, forming an average cover of over 80% by the end of the sampling period in both winter and summer experiments (Figure 5). In control plots *F. vesiculosus* was completely absent. A significant effect of canopy removal was found 20 months after manipulation. No effect of season was found (Table 3A). Analysis of *F. serratus* cover at the same point revealed no effect of canopy removal (Table 3B). Although *F. serratus* canopy did develop in the winter experiment, slower growth meant this was not significantly greater than the low levels found naturally in the control plots (Figure 6).

Survival of Fucus serratus *juveniles in the* Ascophyllum *zone*

The survival of *F. serratus* juveniles in the *Ascophyllum* zone was significantly lower in plots where the canopy was removed compared to the controls in both the winter and summer experiments (SNK multiple comparisons of significant canopy/season interaction; Table 4, Figure 7). The effect of season on survival was evident only in the canopy removal treatment, with significantly lower survival in the summer. Levels of survival beneath an intact canopy were high in both experiments. Examination of control plots three years after the beginning of the experiment showed that 25% of juveniles were still alive, the largest of these being 18 cm in

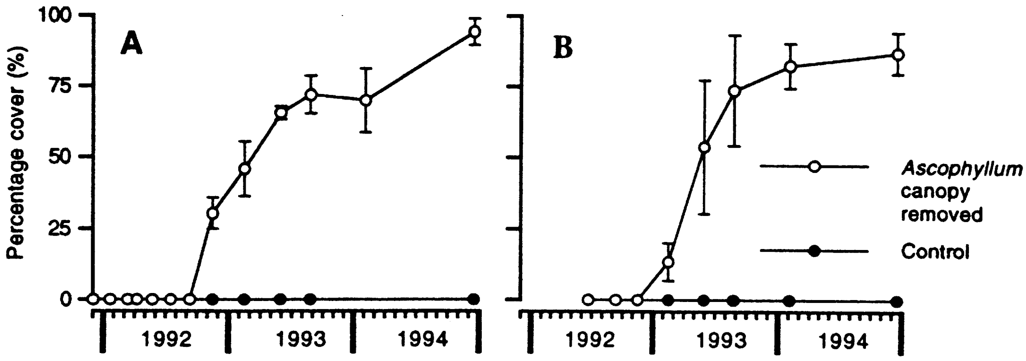

Figure 5. Development of *Fucus vesiculosus* canopy following removal of *Ascophyllum*: (A) winter experiment; (B) summer experiment. Error bars: ±1 SE.

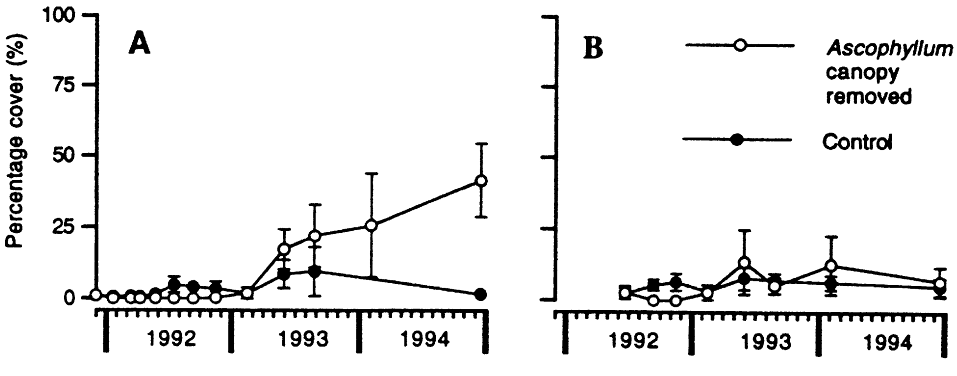

Figure 6. Development of *Fucus serratus* canopy following removal of *Ascophyllum*: (A) winter experiment; (B) summer experiment. Error bars: ±1 SE.

https://doi.org/10.1017/S0025315498000381 Published online by Cambridge University Press

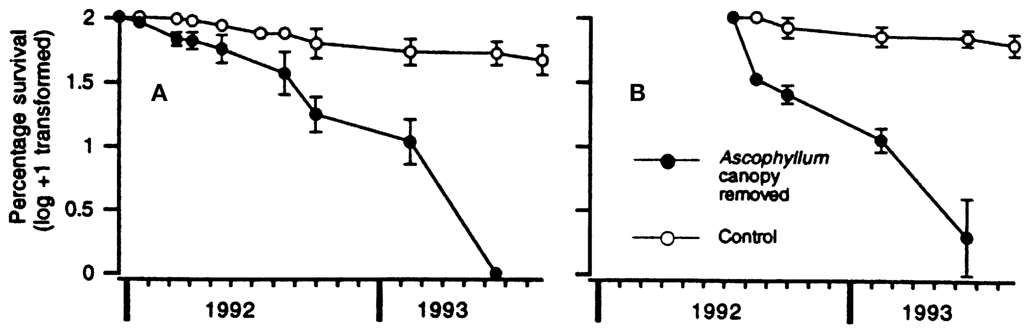

Figure 7. Percentage survival (log + 1 transformed) of *Fucus serratus* juveniles in the *Ascophyllum* zone following canopy clearance: (A) winter experiment; (B) summer experiment. Error bars: ±1 SE.

Table 4. *ANOVA of* Fucus serratus *juvenile survival rates. Percentage survival data, log+1 transformed and regressed against time. Analysis performed using regression coefficients for each replicate as dependent variables.*

Source	df	Mean square	*F*-value	*P*-value
Canopy	1	3.535×10^{-5}	122.120	0.0001
Season	1	3.366×10^{-6}	11.627	0.0092
Canopy × season	1	3.574×10^{-6}	12.347	0.0079
Error	8	2.895×10^{-7}		

SNK multiple comparison tests of interaction between canopy and season

	Winter	Summer
Canopy vs no canopy	s	s
	Canopy	No canopy
Winter vs summer	ns	s

s, significant; ns, not significant.

length. However, grazing damage caused by *Littorina obtusata* was extensive.

Growth rate of Fucus serratus *juveniles in the* Ascophyllum *zone*

The relative growth rate of *F. serratus* juveniles beneath the *Ascophyllum* canopy showed a distinct summer/winter cycle, with very low growth in winter rising to peaks in June 1992 and July 1993 (Figure 8). This simple pattern was not evident in areas cleared of canopy. Early in the year the mean relative growth rate of juveniles in cleared plots was over three times greater than in the control. However, in April the relative growth rate in cleared areas decreased sharply to a level lower than that under the canopy. This decline in growth rate, coincided with the development of a dense cover of green ephemeral species in treatment plots. Despite this the mean relative growth rate calculated over a 14 month period was significantly higher in the cleared plots (Table 5).

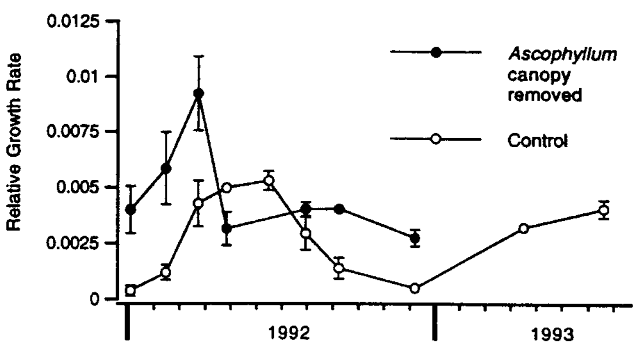

Figure 8. Relative growth rate of *Fucus serratus* juveniles in the *Ascophyllum* zone. Error bars: ±1 SE.

Table 5. *ANOVA of the relative growth rate of* Fucus serratus *juveniles in the* Ascophyllum *zone over the period 18 December 1991 to 5 February 1993.*

Source	df	Mean square	*F*-value	*P*-value
Canopy	1	9.901×10^{-6}	16.66	0.151
Error	4	2.378×10^{-6}		

Comparison of Fucus serratus *juvenile growth rate between the* Ascophyllum *and* F. serratus *zones*

The relative growth rate of *F. serratus* juveniles showed no significant difference between the *Ascophyllum* and *F. serratus* zones (Table 6, Figure 9). There was however a significant difference between quadrats within a zone, indicating variation in the growth rate of juveniles on a spatial scale of between 5 and 20 m. This variation was found predominantly in the *F. serratus* zone (Figure 9). Examination of *F. serratus* juveniles in March 1993 revealed a significantly higher incidence of grazing damage in the *Ascophyllum* zone (one-way ANOVA, $P=0.026$).

Table 6. *ANOVA of the relative growth rate of* Fucus serratus *juveniles in the* Ascophyllum *and* F. serratus *zones.*

Source	df	Mean square	*F*-value	*P*-value
Zone	1	7.331×10^{-5}	3.061	0.155
Quadrat (zone)	4	2.395×10^{-5}	4.672	0.003
Error	42	5.127×10^{-6}		

https://doi.org/10.1017/S0025315498000381 Published online by Cambridge University Press

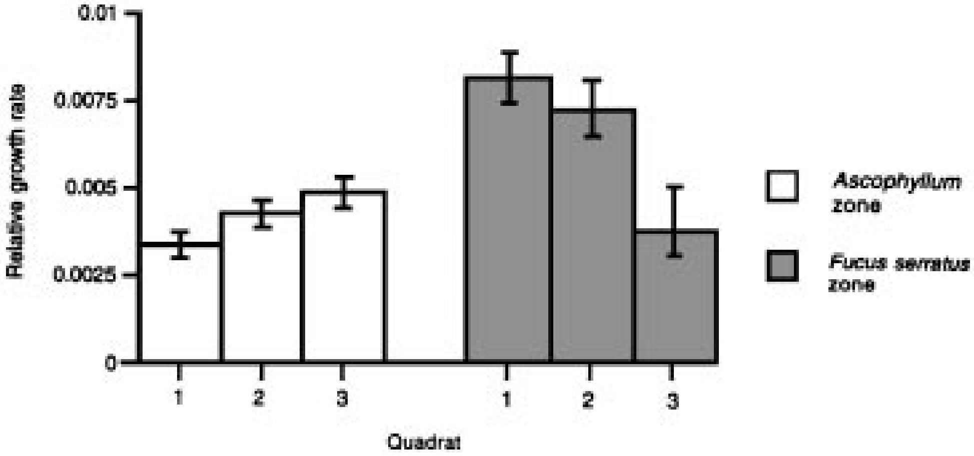

Figure 9. Mean relative growth rate of *Fucus serratus* juveniles in the *F. serratus* and *Ascophyllum* zones. Error bars: ±1 SE.

DISCUSSION

The distribution of fucoid juveniles in the *Ascophyllum* zone and their development in the presence and absence of the dominant *Ascophyllum* canopy give an insight into the patterns of adult canopy species over the mid shore of sheltered and semi-sheltered sites. Lewis (1964) observed great variability in the proportions and zoning of the three competing species of the mid shore, *Ascophyllum*, *Fucus serratus* and *F. vesiculosus*. Although much of this variability can be explained by variations in substrate type, it is proposed here that a consideration of the disturbance regime on sheltered shores will aid an understanding of adult distribution.

Ascophyllum is restricted in its distribution to sheltered and semi-sheltered sites (Lewis, 1964), probably because of the inability of its zygotes to settle in areas of increased wave action (Vadas et al., 1990). Even where it is dominant, juveniles are scarce (Oltmanns, 1889; David, 1943; Knight & Parke, 1950; Printz, 1956; Baardseth, 1970) or very patchily distributed (Aberg & Pavia, 1997). It is a common observation in experimental studies that canopy algae inhibit recruitment of juveniles of the same species (e.g. Chapman, 1989; Benedetti-Cecchi & Cinelli, 1992). Removal of the *Ascophyllum* canopy in this study resulted in high levels of *Ascophyllum* juvenile recruitment, supporting the hypothesis that the canopy is in some way responsible for limiting the density of juveniles in mature stands. Similar enhancement of recruitment was described by Keser (1981) and Keser & Larson (1984) working in Maine, North America but other studies carried out in Europe found only low levels of *Ascophyllum* recruitment following canopy removal (e.g. Knight & Parke 1950). The mechanism by which the *Ascophyllum* canopy inhibits juvenile recruitment was not investigated but most studies of this type attribute enhanced juvenile recruitment following canopy removal to light stimulation (e.g. Santelices & Ojeda, 1984; Robertson, 1987). However, other factors such as a reduction of sweeping (e.g. Velimirov & Griffiths, 1979) and an increase in nutrient availability (Dayton et al., 1984) following canopy removal have been put forward. *Ascophyllum* removal may influence recruitment indirectly through its effect on grazer populations. Limpets were present in small patches throughout the *Ascophyllum* zone but canopy removal had no effect on their density (Jenkins, 1995). Cervin & Aberg (1997) have suggested that isopods and amphipods could be responsible for the extreme mortality of *Ascophyllum* germlings during the first few weeks after settlement. Although no observations were made it is likely that the density of these abundant herbivores will decrease with canopy removal.

Although juvenile recruitment following canopy removal was high, a very low growth rate meant *Ascophyllum* failed to redominate the clearance plots. Five years after the original canopy was removed, the maximum height reached by juveniles was only 20 cm, less than half the height of the dominant *Fucus* canopies. Keser & Larson (1984) showed that in North America *Ascophyllum* juveniles can grow up through a *Fucus* canopy to eventually replace it over this time-scale. Our work showed that the density of *Ascophyllum* juveniles continued to increase long after a canopy of *Fucus* had formed. A much longer period of study will be required to establish whether *Ascophyllum* eventually redominates the experimental plots.

Despite its low growth rate and low recruitment, *Ascophyllum* is very successful. It is the dominant canopy alga on the mid shore across much of its geographical distribution. At four sheltered shores on the Isle of Man *F. vesiculosus* is almost completely excluded from the undisturbed *Ascophyllum* zone. In contrast, *F. serratus*, a low shore species, occurs in small patches or as a sub-canopy. Of the two *Fucus* species with which *Ascophyllum* competes (David, 1943) only *F. serratus* juveniles occurred beneath the intact canopy. These juveniles showed very low rates of growth, although measurements made lower on the shore showed that similar low levels could occur beneath the *F. serratus* canopy. Examination of *F. serratus* juveniles in the low and mid shore revealed a higher degree of grazing damage in the *Ascophyllum* zone. This is probably a result of *F. serratus* individuals being held in the juvenile state beneath the *Ascophyllum* canopy for long periods combined with the higher density of the grazer *Littorina obtusata* in the mid shore (Williams, 1990). This species grazes on macroalgal tissue, in contrast to *Littorina mariae*, the predominant grazer on *F. serratus* in the low shore, which grazes on epiphytes (Watson & Norton, 1987). The low growth rate of *F. serratus* beneath an intact *Ascophyllum* canopy, combined with the grazing pressure of *L. obtusata*, meant that after three years none of the 45 monitored individuals had reached a size at which they were likely to become reproductive (Knight & Parke, 1950).

In the mid shore *F. serratus* appears unable to grow up through an intact, undisturbed *Ascophyllum* canopy but also has only limited ability to colonize cleared areas. In both winter and summer clearance experiments, *F. serratus* juveniles already present beneath the *Ascophyllum* canopy died following canopy removal, probably because of desiccation. This contrasts with the situation low on the shore, where removal of the dominant canopy of *F. serratus* allowed juveniles already present to increase in growth rate and replace the original canopy (Jenkins, 1995). The ability of juveniles to persist beneath a canopy with little or no growth for long periods and then to respond rapidly to gap formation has been observed in both terrestrial forests (Silvertown, 1982) and macroalgal stands (e.g. Dayton et al., 1984; Santelices & Ojeda, 1984). Juveniles of *F. serratus* appear to persist with very low growth beneath the *Ascophyllum* canopy but in the mid shore are unable to cope with the desiccation stress after large-scale canopy removal.

Fucus serratus did colonize cleared areas of the winter experiment by recruitment of new propagules. The period of fertility in this species is between November and May on Manx shores (Creed, 1993). However, canopy development was slower and ultimately at a lower level than *F. vesiculosus* which is fertile in the spring and summer (Creed, 1993). *Fucus vesiculosus*, unlike *F. serratus* was not visibly present beneath the undisturbed *Ascophyllum* canopy. It is a common observation in many algal species that the period of peak propagule production and appearance of juvenile plants can be separated by some time (Hoffmann & Santelices, 1991) owing to a delay in development. This bank of microscopic forms has been considered analogous to the seed banks of land plants. Evidence does exist for a bank of microscopic juveniles in populations of *F. vesiculosus* on exposed shores (Knight & Parke, 1950; Creed et al., 1996). However, the complete absence of this species in the undisturbed *Ascophyllum* communities examined would suggest that it does not exist, and that colonization of the winter experiment occurred via settlement of propagules in the early spring.

Fucus vesiculosus formed a dominant canopy in the winter experiment despite not being fertile at the time of *Ascophyllum* removal. This demonstrates the opportunistic nature and competitive ability of *F. vesiculosus* at mid shore level. In a comparison of the biology of *F. serratus* and *F. vesiculosus* on Manx shores, Knight & Parke (1950) demonstrated the growth rate of *F. serratus* to be approximately twice that of *F. vesiculosus* when situated in their own zones. The importance of growth rate in determining the outcome of competition between benthic macroalgae is well established (see Paine, 1990), thus implying that overgrowth and shading are the major competitive mechanisms. Unfortunately no comparative measures of the growth rate of *F. serratus* and *F. vesiculosus* in the *Ascophyllum* zone were made in this study. It seems likely, in the light of the results on canopy development, that the growth rate of *F. vesiculosus* in cleared areas is higher than *F. serratus*. Surprisingly no significant difference in the growth rate of *F. serratus* juveniles beneath an intact canopy was found between low and mid shore. However, differences are much more likely to be found in areas cleared of the protecting canopy.

Given the apparent competitive superiority of *F. vesiculosus* over *F. serratus* on the mid shore, why does the low shore species *F. serratus* and not *F. vesiculosus* occur naturally in the *Ascophyllum* zone? The scale of a disturbance event can have radical effects on the species composition of succession (Sousa, 1985). The presence of juveniles of *F. serratus* and not of *F. vesiculosus* beneath the natural canopy may indicate a difference in shade tolerance between the two species. Results from monitoring of growth rates of *F. serratus* juveniles indicate that they will not grow to form canopy plants whilst under a full canopy of *Ascophyllum*. However, the loss of one *Ascophyllum* plant, a level of disturbance appropriate to the sheltered shore under study, will increase light levels without causing high levels of desiccation and thus may allow the localized formation of a patch of *F. serratus* within the *Ascophyllum* canopy. The scale of disturbance required for the recruitment of *F. vesiculosus* is probably of a different magnitude, and one which may be found on slightly more exposed shores where *Ascophyllum* gradually gives way to *F. vesiculosus*. Canopy thinning experiments using a range of scales of disturbance, from the removal of one *Ascophyllum* plant upwards, are required to test this hypothesis.

This study is part of a PhD thesis carried out at the University of Liverpool's Port Erin Marine Laboratory and funded by the Natural Environment Research Council. Data analysis and write up were supported by the Mast III project Eurorock MAS3-CT95-0012.

REFERENCES

Aberg, P., 1992. A demographic-study of two populations of the seaweed *Ascophyllum nodosum*. *Ecology*, **73**, 1473–1487.

Aberg, P., 1996. Patterns of reproductive effort in the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series*, **138**, 199–207.

Aberg, P. & Pavia, H., 1997. Temporal and multiple scale variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series*, **158**, 111–119.

Baardseth, E., 1970. Synopsis of biological data on knobbed wrack *Ascophyllum nodosum* (L.) Le Jolis. *FAO Fisheries Synopsis*, 38.

Benedetti-Cecchi, L. & Cinelli, F., 1992. Effects of canopy cover, herbivores and substratum type on patterns of *Cystoseira* spp. settlement and recruitment in littoral rockpools. *Marine Ecology Progress Series*, **90**, 183–191.

Cervin, G. & Aberg, P., 1997. Do littorinids affect the survival of *Ascophyllum nodosum* germlings? *Journal of Experimental Marine Biology and Ecology*, **218**, 35–47.

Chapman, A.R.O., 1989. Abundance of *Fucus spiralis* and ephemeral seaweeds in a high eulittoral zone: effects of grazers, canopy and substratum type. *Marine Biology*, **102**, 565–572.

Chapman, A.R.O., 1990. Competitive interactions between *Fucus spiralis* L. and *F. vesiculosus* L. (Fucales, Phaeophyta). *Hydrobiologia*, **204/205**, 205–209.

Cousens, R., 1986. Quantitative reproduction and reproductive efforts by stands of the brown alga *Ascophyllum nodosum* (L.) Le Jolis in south eastern Canada. *Estuarine and Coastal Shelf Science*, **22**, 495–507.

Creed, J.C., 1993. *Intraspecific competition in seaweeds*. PhD thesis, University of Liverpool.

Creed, J.C., Norton, T.A. & Kain, J.M., 1996. Are neighbours harmful or helpful in *Fucus vesiculosus* populations? *Marine Ecology Progress Series*, **133**, 191–201.

David, H.M., 1943. Studies in the autecology of *Ascophyllum nodosum* Le Jol. *Journal of Ecology*, **31**, 178–198.

Dayton, P.K., 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs*, **45**, 137–159.

Dayton, P.K., Currie, V., Gerrodette, T., Keller, B.D., Rosenthal, R. & Ven Tresca, D., 1984. Patch dynamics and stability of some California kelp communities. *Ecological Monographs*, **54**, 253–289.

Evans, G.C., 1972. *The quantitative analysis of plant growth*. Oxford: Blackwell Scientific Publications.

Hawkins, S.J. & Hartnoll, R.G., 1985. Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series*, **20**, 265–271.

Hawkins, S.J., Hartnoll, R.G., Kain, J.M. & Norton, T.A., 1992. Plant animal interactions on hard substrata in the north-east Atlantic. In *Plant–animal interactions in the marine benthos* (ed. D.M. John et al.), pp. 1–32. Oxford: Clarendon Press.

Hoffmann, A.J. & Santelices, B., 1991. Banks of algal microscopic forms: hypotheses on their functioning and comparisons with seed banks. *Marine Ecology Progress Series*, **79**, 1–2.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.

Jenkins, S.J., 1995. *The ecology of sheltered, canopy dominated shores*. PhD thesis, University of Liverpool.

Josselyn, M.N. & Mathieson, A.C., 1978. Contribution of receptacles from the fucoid *Ascophyllum nodosum* to the detrital pool of a north temperate estuary. *Estuaries*, **1**, 258–261.

Keser, M. & Larson, B.R., 1984. Colonization and growth of *Ascophyllum nodosum* (Phaeophyta) *in Maine. Journal of Phycology*, **20***, 83–87.*

Keser, M., Vadas, R.L. & Larson, B.R., 1981. Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Maine, U.S.A. *Botanica Marina*, **24**, 29–38.

Knight, M. & Parke, M.W., 1950. A biological study of *Fucus vesiculosus* and *Fucus serratus*. *Jounal of the Marine Biological Association of the United Kingdom*, **29**, 439–514.

Lewis, J.R., 1964. *The ecology of rocky shores*. London: English Universities Press.

Oltmanns, F., 1889. Beitrage zur Kenntnis der Fucaceen. *Bibliotheca Botanica*, **14**, 1–94.

Paine, R.T., 1990. Benthic macroalalgal competition: complications and consequences. *Journal of Phycology*, **26**, 12–17.

Printz, H., 1956. Recuperation and recolonisation in *Ascophyllum nodosum*. *Proceedings of the International Seaweed Symposium*, **2**, 194–197.

Reed, D.C. & Foster, M.S., 1984. The effect of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology*, **65**, 937–948.

Robertson, B.C., 1987. Reproductive ecology and canopy structure of *Fucus spiralis* L. *Botanica Marina*, **30**, 475–482.

Santelices, B. & Ojeda, F.P., 1984. Effects of canopy removal on the understory algal community structure of coastal forests of *Macrocystis pyrifera* from southern South America. *Marine Ecology Progress Series*, **14**, 165–173.

Schonbeck, M.W. & Norton, T.A., 1980. Factors controlling the lower limits of fucoid algae on the shore. *Journal of Experimental Marine Biology and Ecology*, **43**, 131–150.

Sharp, G., 1986. *Ascophyllum nodosum* and its harvesting in eastern Canada. In *Case studies of seven commercial seaweed resources* (ed. J.F. Caddy et al.), pp. 3–48. Rome: FAO. [FAO Fisheries Technical Paper.]

Silvertown, J.W., 1982. *Introduction to plant population ecology*. London: William Clowes Ltd.

Sousa, W.P., 1985. Disturbance and patch dynamics on rocky intertidal shores. In *The ecology of natural disturbance and patch dynamics* (ed. S.T.A. Pickett and P.S. White), pp. 101–124. New York: Academic Press.

Underwood, A.J., 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge: Cambridge University Press.

Vadas, R.L., Wright, W.A. & Miller, S.L., 1990. Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Marine Ecology Progress Series*, **61**, 263–272.

Velimirov, B. & Griffiths, C.L., 1979. Wave-induced kelp movement and its importance for community structure. *Botanica Marina*, **22**, 169–172.

Watson, D.C. & Norton, T.A., 1987. The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli. *Journal of Experimental Marine Biology and Ecology*, **112**, 61–72.

Williams, G.A., 1990. The comparative ecology of the flat periwinkles *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli. *Field Studies*, **7**, 469–482.

Submitted 18 July 1997. Accepted 24 February 1998.