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Long term effects of *Ascophyllum nodosum* canopy removal on mid shore community structure

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The long term effects of macroalgal canopy removal on community composition were investigated over a 12 year period. Experimental removal of the dominant *Ascophyllum nodosum* canopy led to short term changes in community composition, the major features of which were still apparent 12 years later. *Ascophyllum* was slow to recover despite high recruitment, and experimental plots were dominated by *Fucus* species. After 12 years a mixed assemblage of *Fucus serratus*, *Fucus vesiculosus* and *Ascophyllum* had developed. Canopy removal resulted in a change in the balance between grazing limpets and the cover of red algal turf in the understorey community. The cover of turfing algae declined significantly allowing the area grazed by limpets to extend. This led to a 3–6 fold increase in the limpet population 12 years after canopy removal.

INTRODUCTION

Physical disturbance in the intertidal and shallow subtidal zones is frequently manifested as an extensive loss of macroalgal canopy cover (see Underwood, 1998, for discussion), which can have severe effects on the wider community. Canopy algae alter the physical environment at the substratum through the lowering of light levels, amelioration of physical extremes, reduction of water movement and by the physical abrasion of sweeping algal fronds (see Jenkins et al., 1999). Experiments to determine community level effects of canopy loss typically extend over limited periods, rarely more than three years, during which time recovery to the pre-disturbance state frequently fails to occur. Thus, it has not been possible to determine the long-term implications of canopy loss (but see Driskell et al., 2001 for recovery of *Fucus gardneri* over a seven year period).

Ascophyllum nodosum is a long lived canopy alga with an extensive distribution throughout the North Atlantic. At sheltered sites in north-western Europe, *Ascophyllum* forms a near monospecific cover over much of the mid shore. Because of its commercial importance, a number of studies have investigated the potential of *Ascophyllum* for regrowth or recolonization in harvested or experimentally denuded areas (e.g. Printz, 1956; Keser & Larson, 1984) but examination of the community level effects of *Ascophyllum* loss has received less attention. Jenkins et al. (1999) described the important structuring role of the *Ascophyllum* canopy at the mid tide level of a sheltered site in the Isle of Man, and speculated on the long-term implications of canopy loss. We aimed to re-sample the original experiment 12 years after it was established to determine the long-term impact of canopy removal on this community.

MATERIALS AND METHODS

The study site selected, on the Langness peninsula, was typical of the sheltered rocky shores of the south of the Isle of Man with an almost complete cover of fucoid canopy algae (see Jenkins et al., 1999 for complete description of the shore). At mid tide level the shore was dominated by *Ascophyllum nodosum* with small patches of *Fucus vesiculosus* and *Fucus serratus*. The understorey community can be divided into two separate functional units: a multi-species, sediment trapping red algal turf, interspersed with patches of substratum, kept clear of erect algae by the grazing of *Patella vulgata*. These 'bare' patches consisted of a mosaic of bare rock and encrusting algae, predominantly *Phymatolithon lenormandii*, and will subsequently be referred to as 'bare substratum'.

In November 1991 a two-way factorial experiment was established at mid shore level (3.3 m to 4.3 m above lowest astronomical tide) to investigate the effect of the *Ascophyllum* canopy and the limpet, *Patella vulgata*, on the understorey community. Both factors had two levels, presence and absence, resulting in four orthogonal treatments with three replicates. Twelve plots were chosen, all positioned at least five metres apart in areas of smooth, gently sloping topography with a dense cover of *Ascophyllum*. At each plot an area 2×2 m square was measured and the four treatments were assigned at random to the 12 plots. For full details of the experimental set up see Jenkins et al. (1999).

Plots were initially sampled at approximately six week intervals for a period of two years. Thereafter, sampling was undertaken at irregular intervals over the next four years until June 1997. A 0.5×0.5 m quadrat, subdivided into 25 equal squares was placed at four random positions within each plot. These four subsamples were used to calculate a mean value for each replicate. The percentage cover of dominant algal species, 'bare substratum' and number of grazers was estimated.

In June 2003, almost 12 years after establishment of the experiment, and six years after the last sampling point, it was located and re-sampled. Owing to the lack of a significant effect of limpet grazing reported in Jenkins et al. (1999) the experiment was treated as a simple, single factor canopy removal experiment. For each plot the whole 2×2 m area was sampled using a 0.5×0.5 m quadrat and the percentage cover of canopy species, bare substratum and algal turf estimated. In addition the number of limpets in each plot was counted.

RESULTS

Mean *Ascophyllum* canopy cover in unmanipulated plots was almost 100% over the 12 years of sampling, with cover never dropping below 80% in any individual plot. After removal, the *Ascophyllum* canopy showed no recovery over the first six years of the experiment, although recruitment of juveniles was relatively high. Subsequent growth of these recruits has resulted in partial recovery of the original canopy to a mean cover of 46% (Figure 1). This was still significantly lower than in control plots (one-way analysis of variance [ANOVA], arc-sine transformation: $F_{(1,6)}=9.3$, $P<0.025$). The *Fucus* canopy species, that quickly replaced *Ascophyllum* after its original removal, have shown contrasting fortunes over the past six years. *Fucus vesiculosus* has declined to a level approaching that in the control plots, with a mean cover of just under 20%. In contrast, *Fucus serratus* has maintained the same cover it showed in June 1997, with an average of approximately 50%. Thus, 12 years after originally removing the dominant *Ascophyllum* canopy cover, a mixed canopy of *Fucus serratus* and *Ascophyllum*, with occasional *Fucus vesiculosus* plants has developed.

The balance between the cover of red algal turf and bare substratum, in plots where the canopy was removed, has changed markedly. This balance was originally investigated over the first two years of the experiment by measuring the change in size of patches of bare substratum. Twelve years on from the establishment of the experiment it was not possible to sample these original patches in canopy removal plots owing to the large scale breakdown of the red algal turf. Therefore comparison between the cover of bare substratum in the first two years of the experiment and 12 years later has been made by estimating cover in random quadrats as described above. Where the canopy was removed the mean percentage cover of bare substratum has increased from a mean value of 13% over the first two years of the experiment to 49% in 2003 (Figure 2). Comparison of photos of experimental plots between 1991 and 2003 shows that large areas that were covered with a thick turfing algae have become denuded and now support only lithothamnion species and sparse red algae, principally *Chondrus crispus*. In 2003 cover of bare substratum where the canopy was removed was seven times greater than in control plots (one-way ANOVA: $F_{(1,5)}=101.6$, $P<0.001$).

The density of limpets in June 2003 varied significantly between the two experimental treatments with a mean of 23.2 adult limpets (over 15 mm length) per metre square where the canopy was removed compared with only 3.7 per metre square in control plots (one-way ANOVA: $F_{(1,5)}=57.9$, $P<0.001$). Although data on limpet density for experimental plots are not available from 1991, a survey of the mid shore zone at the experimental site showed that the mean density of adult limpets was only 7.4 per metre square. Thus in 2003, adult limpet density in plots where *Ascophyllum* was removed showed six times the density of control plots and three times that in the natural community.

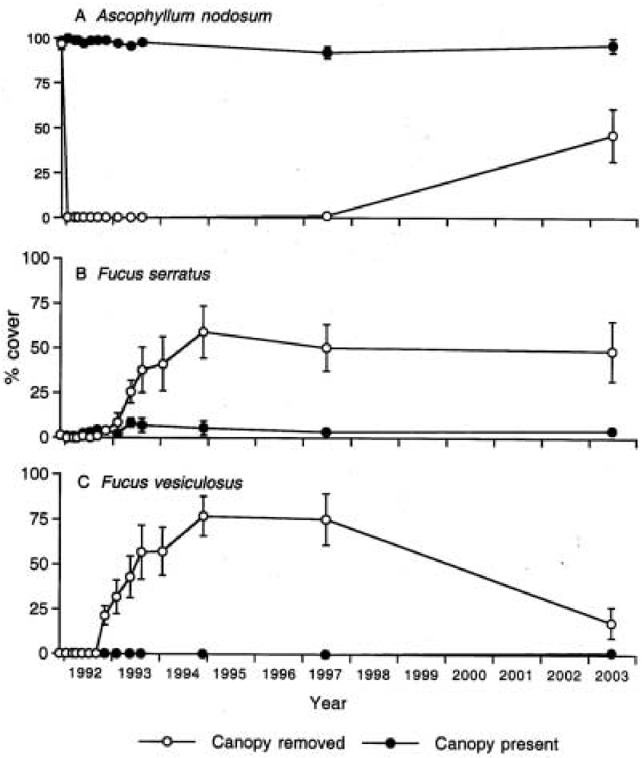

Figure 1. Mean percentage cover of fucoid canopy species (A) *Ascophyllum nodosum*, (B) *Fucus serratus* and (C) *Fucus vesiculosus* after experimental removal of the *Ascophyllum nodosum* canopy. Error bars ±1SE.

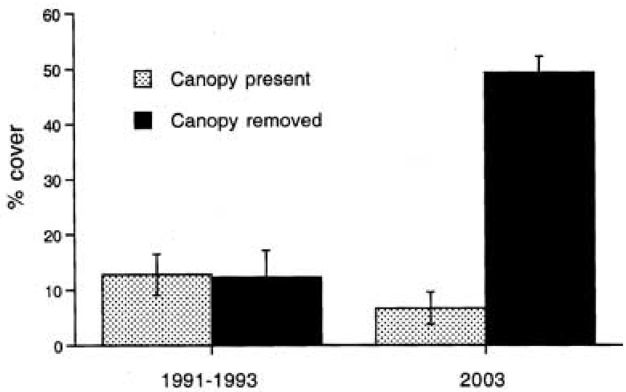

Figure 2. Mean percentage cover of 'bare substratum' composed of bare rock and lithothamnion species after experimental removal of the *Ascophyllum nodosum* canopy. Error bars ±1SE.

DISCUSSION

The partial recovery of the *Ascophyllum* canopy after a 12 year period is consistent with some very early studies on *Ascophyllum* which showed a failure of this species to fully recolonize harvested or experimentally manipulated areas after up to 11 years (Knight & Parke, 1950; Boney, 1965). The general pattern shown by a number of studies into the sustainability of *Ascophyllum* harvesting is one of reduced colonization and growth with increased severity of harvest. Recolonization after holdfast removal relies on new recruitment rather than vegetative regrowth. In this experiment, recruitment level was not a limiting factor (Jenkins et al., 1999) as is commonly suggested, but slow growth and recruitment mortality have clearly limited recovery of the dominant canopy. Limited recovery of the *Ascophyllum* canopy has allowed *Fucus serratus* to dominate experimental plots, although *Fucus vesiculosus* has returned to near background levels. Interestingly *F. vesiculosus* forms a near monospecific band (zone) higher on the shore above *Ascophyllum* while *F. serratus* dominates to form a virtually monospecific canopy below. Thus mature stands of *Ascophyllum* inhibit *F. vesiculosus* from extending in quantity lower on the shore and *F. serratus* from extending upwards (see also Hawkins & Hartnoll, 1985). However, once established these species, especially *F. serratus,* persist. Selective removal of *F. vesiculosus* and *F. serratus* would be required to determine whether they inhibit or facilitate the subsequent recovery of *Ascophyllum*.

Recent interest in alternate stable states in intertidal communities has led to a number of manipulative experiments in *Ascophyllum* dominated communities in north America (Dudgeon & Petraitis, 2001; Bertness et al., 2002), but none have extended beyond a few years. Dudgeon & Petraitis (1999) suggest that because of limited recruitment to large clearances of *Ascophyllum* (4 and 8 m diameter) these will not revert to the original community but will continue to diverge in the long term toward an alternate stable state of barnacles and mussels. However, Bertness et al. (2002) considered the formation of *Ascophyllum* beds highly deterministic. Our results, although limited to a single location and shore level, support the conclusions of Bertness et al. (2002). In the sheltered environment at Langness, recolonization of *Ascophyllum* though slow, does appear to be deterministic.

In contrast to the gradual, though far from complete, return to the original *Ascophyllum* canopy, the understorey community has shown no signs of reverting to its original pre-disturbance state. The understorey community in the *Ascophyllum* beds of the Isle of Man is characterized by a dynamic balance between the grazing of patellid limpets and the space occupancy of a diverse red algal turf. Jenkins et al. (1999) showed that removal of *Ascophyllum* resulted in the breakdown of this balance through degeneration of the turf and expansion of the area grazed by limpets. Recent sampling has shown that the breakdown of this balance, caused predominantly by the bleaching and death of sensitive red algal species soon after canopy removal, was still apparent 12 years on. Cover of the red algal turf was significantly reduced and the density of limpets had increased between three and six fold. A substantial increase in the density of limpets in plots where the canopy was removed suggests a return to the pre-disturbance state is not likely in the medium to long term since limpet grazing is likely to prevent extensive growth of red algae. These observations emphasize the importance of long term experiments in community ecology to fully understand the prolonged effects of physical disturbance.

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