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Scale of impact determines early post-disturbance assemblage structure in subtidal *Fucus* beds in the Baltic Sea (Bornholm, Denmark)

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Disturbances occasionally create gaps of varying sizes in the canopy cover of macroalgae on temperate reefs. This study quantified the size distribution of naturally occurring gaps in a subtidal *Fucus serratus* canopy, and experimentally tested the hypotheses that (i) early post-disturbance abundance of dominant assemblage-formers in the canopy-dominated habitat will depend on the spatial extent of the impact, and (ii) the effects of disturbance on the abundance of dominant assemblage-formers at the edges of large impacted areas will be similar to the effects at small impacted areas. Gaps of up to 6 m diameter accounted for 17% of the habitat and, while small gaps were numerically dominant, all gap size-classes accounted for a similar proportion of habitat. Experimental disturbances (canopy clearing) ranging from 0.6 to 4.8 m diameter caused consistent scale-dependent divergence of assemblage structure after 21 days. Of particular interest was a dense cover (~75%) of filamentous algae in the centres of large ($\geq$1.2 m) clearings. Filamentous algae are widely known to have negative effects on *Fucus* recruitment and growth, and their rapid increase in abundance suggests that future recovery of the *Fucus* canopy could be adversely affected. The abundance of most taxa at the edges of large clearings was either indistinguishable from abundances in small clearings and intact canopy, or intermediate between abundances in these treatments and in the centres of large clearings. Juvenile *Fucus* were, however, more abundant around edges than anywhere else. These experimental outcomes support the model that scale-dependent divergence of assemblage structure is conveyed by an escape from processes associated with edges of the original habitat. I propose that, in the subtidal *Fucus* beds of Bornholm, recovery from large disturbances is restricted to encroachment from the edges because the adjacent canopy suppresses the growth of filamentous algae and thus facilitates regeneration and recruitment of *Fucus*.

Key words: assemblage structure, canopy gaps, disturbance, edge effects, scale-dependence, subtidal *Fucus* bed

Introduction

Disturbances such as waves (Kennelly, 1987*a*; Seymour *et al*., 1989), grazing (Cowen *et al*., 1982; Andrew & Jones, 1990) and pathogens (Cole & Babcock, 1996) occasionally remove the macroalgal canopy that dominates most subtidal temperate reefs to create gaps of various sizes. Macroalgal canopies exert a strong influence on understorey communities by, for example, suppressing the presence of sessile invertebrates (Connell, 2003) and erect macroalgae (Toohey *et al*., 2004; Irving, 2005), while facilitating encrusting algae (Melville & Connell, 2001). The mechanisms behind these canopy effects are diverse and complex, and include many aspects of the physical environment (e.g. light, frond abrasion, sediments and water flow, see review by Dayton, 1985) and a range of physiological and ecological processes such as photosynthesis (Irving *et al*., 2004; Toohey *et al*., 2004), recruitment (Duggins *et al*., 1990; Johnson & Brawley, 1998), grazing (Viejo *et al*., 1999; Konar, 2000) and predation (Petraitis & Dudgeon, 1999; Gagnon *et al*., 2004). Consequently, most understorey taxa are affected when macroalgal canopies are suddenly lost. Effects of canopy loss on understorey taxa can manifest themselves as quickly as in a few days (e.g. Viejo *et al*., 1999; Irving *et al*., 2004) and, therefore, rapidly alter ecological conditions that may affect the assembly of species and subsequently the recovery of the canopy. The early phases of post-perturbation community assembly and the spatial scale of disturbance are linked because the centre of an impacted area may escape processes associated with the original habitat, when the disturbance is sufficiently large (Petraitis & Latham, 1999). In contrast, smaller

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areas of impact will remain under influence from the original habitat through the proximity to its edges.

This study experimentally tested the hypotheses that, in a subtidal canopy-dominated habitat, (i) early post-disturbance abundance of dominant assemblage-formers will depend on the spatial extent of the impact, and (ii) the effect of disturbance on the abundance of dominant assemblage-formers at the edges of large impacted areas will be similar to the effects at small impacted areas. First, however, the size structure and distribution of natural gaps in the habitat, otherwise dominated by a dense canopy cover, was quantified in order to identify the relevant spatial scales for manipulative experimentation.

Materials and methods

Study site

The study was conducted near Svaneke (55°01′48″N; 15°08′45″E) on the east coast of Bornholm (Denmark) in the southern Baltic Sea. The shallow (< 5 m) subtidal zone of this area is predominantly flat to gently sloping granite bedrock, with boulders covered by a dense canopy of *Fucus serratus* (*Fucus* hereafter) occasionally broken by gaps of various sizes (Thomsen & Wernberg, 1995). Water motion is wind-driven as there are no lunar tides around Bornholm. The salinity is low but constant around 7–8 psu, and the water temperature range is 2–20°C over the annual cycle.

Natural gaps

The size structure and frequency of gaps in the *Fucus* canopy were quantified by determining the distances and depths where gaps started and ended along transects perpendicular to the coastline. Three 60-m transects were sampled 15–20 m apart at each of four locations (Boelshavn, Vige Havn, Maageflejl, Aarsdale) separated by 3–5 km. All gaps larger than ~30 cm were sampled. Transects were shorter if the *Fucus* zone ended before 60 m.

Clearing experiment

To test the effect of spatial extent of disturbance on the early assembly of major benthic community components, a canopy clearing experiment was carried out at two locations (Vige Havn and Maageflejl) approximately 3 km apart. The areas of canopy removed were 0, 0.3, 1.1, 4.5 and 18.1 m^2 (the 0 m^2 'clearings' were control plots where the canopy was left intact). These sizes covered the range of naturally occurring gaps in the canopy. Three replicates of each clearing size were established at each site at a depth of 2–3 m in August 2004. The clearings were executed as circles of 0, 0.6, 1.2, 2.4 and 4.8 m diameter, and the canopy was removed by cutting stipes immediately above the holdfast. Clearings were sampled after 21 days. The percent cover of taxa was estimated by the 'point-intercept' method (25 evenly spaced grid-intersections within a 20×20 cm quadrat) in the centre of all clearings. The density of herbivorous gastropods and juvenile *Fucus* (< 5 cm) was also determined within the 20×20 cm quadrat. To test for edge-effects, similar measurements were made at the edges (outer 0.3 m perimeter) of large clearings (1.2, 2.4 and 4.8 m). Taxa were identified as morphological groups (herbivorous gastropods, juvenile *Fucus*, filamentous, encrusting and foliose algae, and *Mytilus*) because it was not possible to distinguish many species *in situ*. However, due to the low salinity, the species pool was limited (Voipio, 1981) and most groups comprised only 1–4 possible species. Specifically, the herbivorous gastropods were predominantly of two species, *Littorina littorea* and *Rissoa membranacea*. Filamentous algae were dominated by *Cladophora rupestris*, *C. glomerata* and *Pilayella littoralis*. Only two species of foliose algae were registered, *Fucus serratus* and *Furcellaria lumbricalis*, the latter in only two quadrats. Encrusting algae were predominantly *Hildenbrandia rubra* and *Ralfsia verrucosa*. Other categories included the common blue mussel (*Mytilus edulis*, hereafter *Mytilus*), loose sediments (sand and gravel) and bare rock. Due to physiological stress caused by the brackish waters of the Baltic Sea, both gastropods (*Littorina* max length ~1.0 cm) and mussels (*Mytilus* max length ~3 cm) were severely reduced in size relative to their conspecifics in fully marine environments (Voipio, 1981).

Data analysis

The proportion of habitat occupied by gaps was calculated for each transect, and differences among locations tested with one-way ANOVA. Transects were then pooled within locations and the number of gaps tallied in 0.3 m size classes. The total extent of gaps at each location was calculated by summing all gaps within a size class. One-way ANOVA tested for differences in frequency and total extent (distance) of gaps between size-classes, before converting these to percentages for presentation. Product moment correlation tested for a relationship between gap size and depth, combining gaps from all transects. Data collected in the clearing experiment were analysed with mixed model ANOVA with location (random) and clearing size (fixed) as orthogonal factors. Four *a priori* planned contrasts (*a*: 0, 0.6, 1.2 and 2.4 *v*. 4.8; *b*: 0, 0.6 and 1.2 *v*. 2.4; *c*: 0 and 0.6 *v*. 1.2; *d*: 0 *v*. 0.6) identical to those used by Petraitis *et al.* (2003) tested the presence of thresholds in abundance of taxa with increasing clearing size. Edge effects were tested with three *a priori* planned contrasts following a separate one-way fixed factor ANOVA of all treatments (centres of five clearing sizes and edges from three clearings ≥ 1.2 m) at both locations. The first contrast compared the edges of large clearings (≥ 1.2 m) between the two locations (effects of location on centre samples were tested in the first ANOVA). The second contrast compared edges of large clearings to their centres. This contrast did not consider the paired nature of centres and edges. However, neither non-independence of paired samples nor increased risk of type II error was an issue in the current experiment because there was no correlation between paired samples for any taxa (Product moment correlation, $-0.05 < r < 0.34$, $p > 0.17$, $n = 18$) and all contrasts were highly significant. The third contrast compared edges of large clearings to small clearings (0.6 m). Taking all taxa into account, similarities in assemblage structure among centres of large clearings, their edges, small clearings and intact canopy were graphed in a nMDS plot based on Bray–Curtis similarities. Multivariate differences among these groups were tested with one-way ANOSIM and subsequent pair-wise comparisons.

Results

Size distribution of natural gaps

There were no differences among the four locations in the proportion of habitat within the *Fucus* belt occupied by gaps in the canopy cover ($F_{(3,8)} = 2.88$, $p = 0.103$) and the mean was 17.3% ± 1.8 (SE; $n = 4$). Small gaps were numerically dominant (Fig. 1A; Log(x+1) transformed data, $F_{(9,30)} = 8.56$, $p < 0.001$) and, across all locations, the median and mean gap sizes were 0.7 and 1.1 m, respectively. The largest gap encountered on any transect was 6.0 m. Although small gaps were more abundant than larger gaps, the total extent of gaps was evenly distributed among gap size classes (Fig. 1B; $F_{(9,30)} = 1.35$, $p = 0.250$). There was no correlation between gap size and depth ($r = 0.05$, $n = 112$).

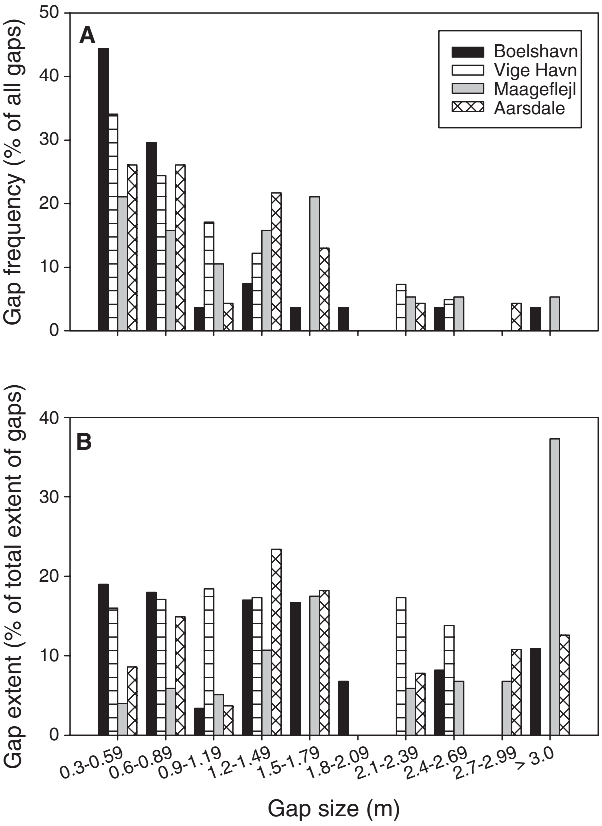

Fig. 1. The frequency of occurrence (A) and extent (B) of gaps in the canopy cover of *Fucus serratus* at four locations, separated by 3–5 km, in the vicinity of Svaneke (Bornholm, southern Baltic Sea). Data for each location are the sum of gaps measured along three 60-m transects perpendicular to the coastline. Boelshavn: $n = 27$ gaps; Vige Havn: $n = 41$ gaps; Maageflejl: $n = 21$ gaps; and Aarsdale: $n = 23$ gaps.

Scale-dependent effects of canopy clearing

There was a highly significant ($p < 0.025$) effect of clearing size on the abundance of filamentous and encrusting algae (Table 1). Clearing size did not have any statistically significant effects on the percentage cover of foliose algae (data not shown) and *Mytilus*, or on the density of herbivorous gastropods and juvenile *Fucus* (Table 1). There were no significant differences in abundances of the quantified taxa between the two locations (Table 1), and all scale-dependent patterns were consistent between the two locations (i.e. no interactions between Location and Size). The planned contrasts showed significant step-wise differences in abundance of filamentous and encrusting algae, and near-significant effects for herbivorous gastropods, *Mytilus* and juvenile *Fucus* (Fig. 2). Filamentous algae were almost three times more abundant in clearings ≥1.2 m than in smaller clearings or under intact canopy. Conversely, encrusting algae were twice as abundant in clearings ≤0.6 m as in larger clearings. Both gastropod densities and percentage cover of *Mytilus* were lower in large (≥2.4 m and ≥1.2 m, respectively) than in smaller clearings, whereas densities of juvenile *Fucus* were higher in all experimental clearings compared to the uncleared controls (Fig. 2). So, despite the lack of statistical significance for an effect of clearing size, there were trends of scale-dependent effects on densities of gastropods and juvenile *Fucus* as well as on percentage cover of *Mytilus*.

Edge effects

There were no effects of location on the abundance of dominant assemblage-formers at the edges of large clearings (≥1.2 m; Table 2). All taxa had significantly different abundances at the edge compared to the centre of large clearings (Fig. 2, Table 2), and the direction of differences between edges and centres was consistent across all large clearing sizes for all taxa (Fig. 2). Juvenile *Fucus* were found in higher densities at the edges of large clearings than anywhere else (Fig. 2), although the difference between edges of large clearings and small clearings was not statistically significant (Table 2). With the exception of juvenile *Fucus*,

Table 1. Results of ANOVA testing for effects of location and clearing size on the abundance of major taxa in the centres of clearings

Source of variation	*df*	*MS*	*F*	*p*	*MS*	*F*	*p*
		Herbivorous gastropods*			Juvenile *Fucus*†		
Location	1	0.021	0.33	0.574	0.023	0.07	0.797
Clearing size	4	0.189	1.86	0.281	0.428	1.76	0.298
Loc × Size	4	0.102	1.57	0.221	0.243	0.72	0.590
Residual	20	0.065			0.339		
		Filamentous algae*			Encrusting algae		
Location	1	0.065	2.25	0.149	154.1	0.89	0.358
Clearing size	4	0.757	11.79	**0.017**	2270.1	9.64	**0.025**
Loc × Size	4	0.064	2.24	0.101	235.5	1.35	0.285
Residual	20	0.029			173.9		
		Mytilus					
Location	1	104.5	1.29	0.270			
Clearing size	4	587.5	2.66	0.183			
Loc × Size	4	220.5	2.72	0.059			
Residual	20	81.1					

Data passed tests of normality (visual inspection of residuals) and equal variances (Cochran's *C*-test, $p > 0.05$).
* Log(X) transformed.
† Log(X + 1) transformed.
Significant *p*-values in bold type.

abundances of taxa at the edges of large clearings were either indistinguishable from abundances in uncleared control plots or small clearings (≤0.6 m; herbivorous gastropods, encrusting algae), or intermediate between these and abundances in the centres of large clearings (filamentous algae, *Mytilus*; Fig. 2, Table 2).

Assemblage structure

The assemblage structure at the centres of large clearings was significantly different ($p = 0.001$) and highly distinct (Clarke's $R > 0.4$, Table 3) from the assemblage structure in uncleared control plots, small clearings and at the edges of large clearings (Table 3). Assemblage structure at the edges of large clearings, on the other hand, was indistinguishable from that of small clearings which, in turn, overlapped with the assemblage structure of control plots (Table 3). Consequently, the assemblage structure of small clearings and at the edges of large clearings was intermediate between that of controls (Fig. 3, right) and the centres of large clearings (Fig. 3, left).

Discussion

This study found that natural gaps of up to several metres across were a prominent feature of the subtidal *Fucus* habitat. Experimentally imposed disturbances, gaps of various sizes up to 4.8 m diameter, caused the early post-disturbance abundance of dominant assemblage-formers and assemblage structure to differ between the centres of small and large impacted areas, but generally not between the edges of large impacts and small impacts. In particular, the substantially higher cover of filamentous algae in large clearings, compared with small clearings, corroborates the first hypothesis, that the early post-disturbance abundance of dominant assemblage-formers depends on the spatial extent of the impact. Similarly, the finding that assemblage structure at the edge of large clearings was intermediate between the assemblage structure of uncleared control plots and those in the centre of large clearings, but indistinguishable from small clearings, corroborates the second hypothesis, that the effects of disturbance at the edges of large impacts are similar to the effects of small impacts. Consequently, this study found support for the model that an escape from edge-associated processes of the original habitat causes scale-dependent differences in the early post-disturbance abundance of organisms.

The presence of abundant gaps in the *Fucus* canopy in late summer indicates either that gaps are readily formed in summer or that gaps formed at other times persist through summer. There are no tides or swell in the Baltic Sea (Voipio, 1981) and large grazers such as sea urchins are absent (Voipio, 1981). Natural disturbances are therefore predominantly caused by wind-driven waves. The locations used in this research face east and, because of a large fetch (> 100 km) and deep water (> 50 m) within ~300 m of the shore, the coast is fully exposed to waves of up to 3–4 m (personal observation) generated by strong winds

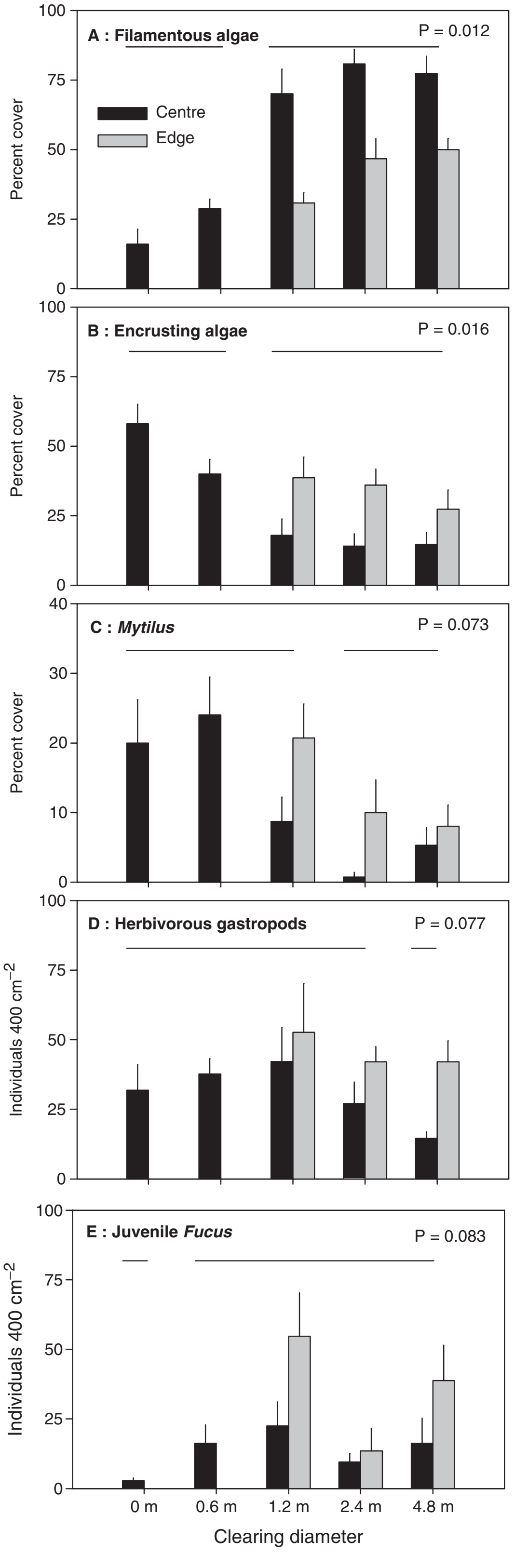

Fig. 2. Abundance of dominant assemblage-formers, determined within a 20×20 cm quadrat, at the centres of experimental clearings and at the edges of large clearings 21 days after impact. Clearings were set up in a subtidal *Fucus serratus* habitat at two locations, 3 km apart, in the vicinity of Svaneke (Bornholm, southern Baltic Sea). Data were pooled across locations as there were no effects of location. Horizontal lines above histograms indicate results from planned contrasts where the *p*-value shows the significance level of the contrast. Error bars are SE ($n = 6$).

from easterly directions. Strong ($> 11\,\mathrm{m\,s^{-1}}$) easterly winds occur 1–2% of the time in summer but more frequently (5–10%) in autumn and winter (Cappelen & Jørgensen, 1999). Consequently, there is potential for gap formation year-round, but winter and autumn are the main seasons for disturbances, as in most other temperate reef systems (Paine & Levin, 1981; Kennelly, 1987*a*; Seymour *et al.*, 1989).

The frequency distribution of sizes of gaps in the *Fucus* canopy was positively skewed (Fig. 1). Similar gap-size distribution patterns have been found in other subtidal (Kennelly, 1987*a*; Irving, 2005) and intertidal (Farrell, 1989; Worm & Chapman, 1998) habitats dominated by canopy algae, and they probably reflect that disturbances occur at small scales (i.e., < 1 m) more frequently than at larger scales. Despite small gaps being numerically dominant, the total amount of habitat occupied by each gap size-class was roughly the same, suggesting that no particular size of gap is disproportionately important in characterizing habitat structure. However, most scale-dependent effects were found for experimental clearings ≥ 1.2 m diameter corresponding to 34.8% of the naturally occurring gaps. Assuming that the canopy-associated processes operating across the edges into natural gaps have a similar scale-dependency as it appears from my experimental gaps, this would imply that 95.6% of the total gap area, or ~16.5% of the entire habitat, are governed by processes different from those associated with the dominant habitat former. This is a conservative estimate because it is based on a one-dimensional surrogate for gap area. In reality, because gaps are 2-dimensional, the area of gaps does not increase linearly with gap size, but follows a power function.

Filamentous and encrusting algae, two growth forms widely known to be associated with gaps and macroalgal canopies, respectively (Reed & Foster, 1984; Ballesteros, 1990; Edwards, 1998; Melville & Connell, 2001; Fowler-Walker & Connell, 2002), showed strong scale-dependent effects. Filamentous algae have repeatedly been shown to negatively affect recruitment of several kinds of canopy algae from both subtidal and intertidal habitats around the world (e.g., Kennelly, 1987*b*; Edwards, 1998; Isaeus *et al.*, 2004). Most importantly, however, several recent experiments have independently shown that filamentous algae – *Cladophora glomerata* and *Pilayella littoralis* among others – can reduce and prevent recruitment and survival of juvenile *Fucus* in the Baltic Sea (Worm *et al.*, 2001; Berger *et al.*, 2003; Eriksson & Johansson, 2003; Isaeus *et al.*, 2004; Råberg *et al.*, 2005). An adverse effect of filamentous algae is consistent with the

Table 2. Results of *a priori* planned contrasts, testing for effects on the abundance of major community constituents of edges of large clearings ($\geq$1.2 m diameter) relative to centres of large clearings, small clearings and uncleared control plots

Source of variation	*df*	*MS*	*F*	*p*	*MS*	*F*	*p*
		Herbivorous gastropods*			Juvenile *Fucus*		
Between treatments	15	0.119	2.0	0.048	994	1.8	0.078
Edge$_{\text{Loc1}}$ *v.* edge$_{\text{Loc2}}$	1	0.058	1.0	0.329	242	0.4	0.511
Edge$_{1.2,\,2.4,\,4.8\text{m}}$ *v.* centre$_{1.2,\,2.4,\,4.8\text{m}}$	1	0.630	10.6	**0.003**	3428	6.2	**0.018**
Edge$_{1.2,\,2.4,\,4.8\text{m}}$ *v.* small$_{0.6\text{m}}$	1	0.013	0.2	0.638	1680	3.1	0.090
Residual	32	0.059			549		
		Filamentous algae			Encrusting algae		
Between treatments	15	1781	9.7	< 0.001	764	3.5	0.002
Edge$_{\text{Loc1}}$ *v.* edge$_{\text{Loc2}}$	1	44	0.2	0.630	257	1.2	0.286
Edge$_{1.2,\,2.4,\,4.8\text{m}}$ *v.* centre$_{1.2,\,2.4,\,4.8\text{m}}$	1	10093	54.8	**< 0.001**	3050	13.9	**0.001**
Edge$_{1.2,\,2.4,\,4.8\text{m}}$ *v.* small$_{0.6\text{m}}$	1	853	4.6	**0.039**	162	0.7	0.396
Residual	32	184			219		
		Mytilus					
Between treatments	15	272	2.8	0.007			
Edge$_{\text{Loc1}}$ *v.* edge$_{\text{Loc2}}$	1	57	0.6	0.450			
Edge$_{1.2,\,2.4,\,4.8\text{m}}$ *v.* centre$_{1.2,\,2.4,\,4.8\text{m}}$	1	574	5.9	**0.021**			
Edge$_{1.2,\,2.4,\,4.8\text{m}}$ *v.* small$_{0.6\text{m}}$	1	555	5.7	**0.023**			
Residual	32	98					

Data passed tests of normality (visual inspection of residuals) and equal variances (Cochran's *C*-test, $p > 0.05$).
*Log(X) transformed.
Significant *p*-values for contrasts in bold type.

Table 3. Results of pair-wise comparisons following ANOSIM testing the effect of clearing size and position within clearings on differences in assemblage structure

Comparison	Clarke's *R*	*P*
Control *v.* Small	0.122	0.063
Control *v.* Large, edge	0.389	0.003
Control *v.* Large, centre	0.803	0.001
Small *v.* Large, edge	–0.058	0.692
Small *v.* Large, centre	0.599	0.001
Large, edge *v.* Large, centre	0.404	0.001

Global $R = 0.41$, $p = 0.001$; 999 permutations.

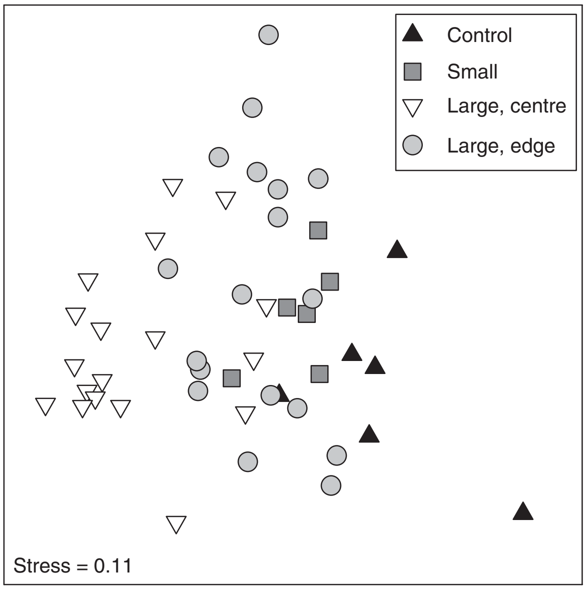

Fig. 3. nMDS plot of similarity of post-disturbance assemblage structure in control plots (intact canopy), small clearings (0.6 m diameter), and centres and edges of large clearings (1.2–4.8 m diameter), 21 days after implementing clearings in the *Fucus serratus* canopy cover near Svaneke (Bornholm, southern Baltic Sea).

significantly higher densities of juvenile *Fucus* found at the edge compared to the centre of large clearings, where the cover of filamentous algae was lower (Fig. 2A, E). The apparent lack of higher densities of juvenile *Fucus* in small clearings (0.6 m), hypothesized to be similar to edges of large clearings, could be due to scale-dependent differences in the physical environment (e.g. light) caused by canopy movement; whereas the edges of large clearings are affected by the adjacent canopy for only half the wave cycle, small clearings are affected over the entire wave cycle (Emmerson & Collings, 1998).

Given the duration of the study, it is unlikely that the juvenile *Fucus* observed represent new recruitment. Rather, they must result from either growth of already settled microscopic recruits (Worm *et al.*, 2001) or regeneration from fragments and old holdfasts. McCook & Chapman (1992) found that 20–30% of *F. vesiculosus* cut within small 0.25 m^2 plots on an intertidal platform would regenerate canopy-forming fronds (~0.25 cm week^{-1}) from the holdfasts, and they speculated that regeneration could be an important mechanism for recovery from disturbances.

This potent ability of *Fucus* to regenerate vegetatively possibly explains the frequent recovery of clearings in *Fucus* beds (e.g. McCook & Chapman, 1992; Speidel *et al.*, 2001) and the ability of *Fucus* to take over, dominate and persist in clearings in other canopy habitats such as *Ascophyllum* beds (e.g. Petraitis *et al.*, 2003; Jenkins *et al.*, 2004). All of these studies, however, were conducted in the intertidal zone. The effect of filamentous algae on regeneration is not known, and neither is the extent to which intertidal studies can be extrapolated to subtidal habitats. For example, contrary to all evidence from subtidal habitats (including several independent studies of *Fucus* from the Baltic Sea, *op. cit.*), some intertidal studies have found ephemeral and filamentous algae to facilitate recruitment of canopy species (McCook & Chapman, 1993, Johnson & Brawley, 1998).

Herbivorous gastropods and *Mytilus* also showed (near-significant) scale-dependent effects of canopy removal, both taxa being less abundant in the centres of large clearings relative to small clearings and edges (Fig. 2). Farrell (1989) also found fewer gastropod grazers in the centres of clearings and explained this in terms of the canopy providing protection against predation. The responses of herbivorous gastropods to canopy loss may however depend on species and time (Worm & Chapman, 1998; Petraitis *et al.*, 2003). The common predators of gastropods and *Mytilus*, crabs and sea stars, are absent from this part of the Baltic Sea (Voipio, 1981) and predation on *Mytilus*, for example, is generally considered to be negligible (Kautsky, 1981). Fish have, however, recently been shown to control *Mytilus* abundance in some parts of the Baltic (Lappalainen *et al.*, 2005), and it is possible that, in newly formed gaps where the canopy no longer offers protection, molluscs become focal points for predation by common fish such as flounder (*Platichthys flesus*) and eelpout (*Zoarches viviparus*).

Considering the short duration of the experiment, some caution is warranted when interpreting effects other than the overwhelming response of filamentous algae. Algae of this growth form are notorious for their rapid growth when resources such as light and nutrients are available (e.g. Pihl *et al.*, 1996; Pedersen *et al.*, 2005), and their presence in the microscopic ‘seedbank’ (Worm *et al.*, 2001) ensures a rapid response when space is released. It is thus possible that the responses of other taxa were due to overgrowth by filamentous algae rather than to changes in cover or density *per se*. Nevertheless, the response of filamentous algae is likely to be of key importance to the subsequent community assembly and recovery due to their widely reported negative effects on recruitment and survival of canopy-formers (*op. cit.*). Dense cover of filamentous algae may also affect other understorey organisms by, for example, retaining sediments and reducing light or oxygen levels.

It is clear that the subtidal *Fucus* habitat of Bornholm is a mosaic of relatively distinct canopy and gap patches, laced by edges that must comprise a substantial area. The ecological processes taking place across these interfaces are important to patch dynamics because gap closure or persistence may be an edge-driven process (Kennelly, 1987*b*; Farrell, 1989; Kennelly & Underwood, 1993; Airoldi, 1998); I found that the abundance of dominant assemblage-formers at the edge of large clearings was similar (herbivorous gastropods, juvenile *Fucus*) to that in small clearings, or intermediate (filamentous algae, *Mytilus*) between these and the centres of large clearings (Fig. 2, Table 2). Similar effects have been reported by Farrell (1989) from the high intertidal of Oregon (USA) and Kennelly & Underwood (1993) from subtidal *Ecklonia radiata* kelp beds in Australia, and these results support the model that the scale-dependent response of centres of large clearings is caused by an escape from edge-effects.

Whether or not the initial divergence of assemblages in small and large gaps can or will lead to persistent alternative assemblages depends on the nature of the subsequent succession (cf. Connell & Slatyer, 1977). If succession facilitates recruitment and regeneration of *Fucus*, gaps will recover to canopy. If, on the other hand, succession inhibits the recruitment and regeneration of *Fucus*, gaps could be maintained in an alternative canopy-free assemblage. Because filamentous algae, as a growth form, are notorious for their negative effects on recruitment and survival of juvenile canopy formers (*op. cit.*), it seems reasonable to predict that the subsequent succession will inhibit *Fucus* in the centres of large clearings. Interestingly, however, juvenile *Fucus* were more abundant at the edges of large clearings than anywhere else, suggesting that these edges may facilitate recovery of the canopy. Speidel *et al.* (2001) found that complete removal of an intertidal *Fucus gardneri* canopy delayed full recovery by several months relative to partial removal ($<80\%$) of the canopy, and concluded that proximity to even a few adult *Fucus* greatly increased the recovery rate. It is therefore possible that abrasion from *Fucus* fronds is needed to suppress the filamentous algae (Kiirikki, 1996; Irving, 2005) that would otherwise inhibit *Fucus* recruitment, regeneration and growth. Hence, it seems likely that the strong scale-dependent increase in filamentous algae in large clearings will retard the canopy recovery process, restricting it to a slow encroachment from the edges.

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References

Airoldi, L. (1998). Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology*, **79**: 2759–2770.

Andrew, N.L. & Jones, G.P. (1990). Patch formation by herbivorous fish in a temperate Australian kelp forest. *Oecologia*, **85**: 57–68.

Ballesteros, E. (1990). Structure and dynamics of the community of *Cystoseira zosteroides* Turner C. Agardh (Fucales, Phaeophyceae) in the Northwestern Mediterranean. *Sci. Mar.*, **54**: 217–230.

Berger, R., Henriksson, E., Kautsky, L. & Malm, T. (2003). Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquat. Ecol.*, **37**: 1–11.

Cappelen, J. & Jørgensen, B. (1999). Observed wind speed and direction in Denmark – with climatological standard normals, 1961–90. Report no. 99-13. Danish Meteorological Institute.

Cole, R.G. & Babcock, R.C. (1996). Mass mortality of a dominant kelp (Laminariales) at Goat Island, North-eastern New Zealand. *Mar & Freshw. Res.*, **47**: 907–911.

Connell, J.H. & Slatyer, R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Nat.*, **111**: 1119–1144.

Connell, S.D. (2003). Negative effects overpower the positive of kelp to exclude invertebrates from the understorey community. *Oecologia*, **137**: 97–103.

Cowen, R.K., Agegian, C.R. & Foster, M.S. (1982). The maintenance of community structure in a central California kelp forest. *J. Exp. Mar. Biol. Ecol.*, **64**: 189–201.

Dayton, P.K. (1985). Ecology of kelp communities. *Ann. Rev. Ecol. Syst.*, **16**: 215–245.

Duggins, D.O., Eckman, J.E. & Sewell, A.T. (1990). Ecology of understorey kelp environments. 2. Effects of kelps on recruitment of benthic invertebrates. *J. Exp. Mar. Biol. Ecol.*, **143**: 27–45.

Edwards, M.S. (1998). Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (Light F). *J. Exp. Mar. Biol. Ecol.*, **228**: 309–326.

Emmerson, L.M. & Collings, G.J. (1998). Macroalgal recruitment in artificially disturbed areas: interactive effects of temporal and spatial scale. *Mar. Freshw. Res.*, **49**: 541–546.

Eriksson, B.K. & Johansson, G. (2003). Sedimentation reduces recruitment success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *Eur. J. Phycol.*, **38**: 217–222.

Farrell, T.M. (1989). Succession in a rocky intertidal community the importance of disturbance size and position within a disturbed patch. *J. Exp. Mar. Biol. Ecol.*, **128**: 57–74.

Fowler-Walker, M.J. & Connell, S.D. (2002). Opposing states of subtidal habitat across temperate Australia: consistency and predictability in kelp canopy–benthic associations. *Mar. Ecol. Prog. Ser.*, **240**: 49–56.

Gagnon, P., Wagner, G. & Himmelman, J.H. (2004). Use of a wave tank to study the effect of water motion and algal movement on displacement of the sea star *Asterias vulgaris* towards its prey. *Mar. Ecol. Prog. Ser.*, **258**: 125–132.

Irving, A.D. (2005). Patterns and responses of benthos to habitat heterogeneity in algal forests of Australasia and Antarctica. Ph.D. Thesis, University of Adelaide, Adelaide.

Irving, A.D., Connell, S.D. & Elsdon, T.S. (2004). Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. *J. Exp. Mar. Biol. Ecol.*, **310**: 1–12.

Isaeus, M., Malm, T., Person, S. & Svensson, A. (2004). Effects of filamentous algae and sediment on recruitment and survival of *Fucus serratus* (Phaeophyceae) juveniles in the eutrophic Baltic Sea. *Eur. J. Phycol.*, **39**: 301–307.

Jenkins, S.R., Norton, T.A. & Hawkins, S.J. (2004). Long term effects of *Ascophyllum nodosum* canopy removal on mid shore community structure. *J. Mar. Biol. Ass. U.K.*, **84**: 327–329.

Johnson, L.E. & Brawley, S.H. (1998). Dispersal and recruitment of a canopy-forming intertidal alga: the relative roles of propagule availability and post-settlement processes. *Oecologia*, **117**: 517–526.

Kautsky, N. (1981). On the trophic role of the blue mussel (*Mytilus edulis* L.) in a Baltic coastal ecosystem and the fate of the organic matter produced by the mussels. *Kieler Meeresforschungen Sonderheft*, **5**: 454–461.

Kennelly, S.J. (1987*a*). Physical disturbances in an Australian kelp community. I. Temporal effects. *Mar. Ecol. Prog. Ser.*, **40**: 145–153.

Kennelly, S.J. (1987*b*). Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. *J. Exp. Mar. Biol. Ecol.*, **112**: 49–60.

Kennelly, S.J. & Underwood, A.J. (1993). Geographic consistencies of effects of experimental physical disturbance on understorey species in sublittoral kelp forests in central New South Wales. *J. Exp. Mar. Biol. Ecol.*, **168**: 35–58.

Kiirikki, M. (1996). Experimental evidence that *Fucus vesiculosus* (Phaeophyta) controls filamentous algae by means of the whiplash effect. *Eur. J. Phycol.*, **31**: 61–66.

Konar, B. (2000). Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. *Oecologia*, **125**: 208–217.

Lappalainen, A., Westerbom, M. & Heikinheimo, O. (2005). Roach (*Rutilus rutilus*) as an important predator on blue mussel (*Mytilus edulis*) populations in a brackish water environment, the northern Baltic Sea. *Mar. Biol.*, **147**: 323–330.

McCook, L.J. & Chapman, A.R.O. (1992). Vegetative regeneration of *Fucus* rockweed canopy as a mechanism of secondary succession on an exposed rocky shore. *Bot. Mar.*, **35**: 35–46.

McCook, L.J. & Chapman, A.R.O. (1993). Community succession following massive ice-scour on a rocky intertidal shore: recruitment, competition and predation during early, primary succession. *Mar. Biol.*, **115**: 565–575.

Melville, A.J. & Connell, S.D. (2001). Experimental effects of kelp canopies on subtidal coralline algae. *Austral Ecol.*, **26**: 102–108.

Paine, R.T. & Levin, S.A. (1981). Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.*, **51**: 145–178.

Pedersen, M.F., Staehr, P.A., Wernberg, T. & Thomsen, M.S. (2005). Biomass dynamics of exotic *Sargassum muticum* and native *Halidrys siliquosa* in Limfjorden, Denmark – implications of species replacements on turnover rates. *Aquat. Bot.*, **83**: 31–47.

Petraitis, P.S. & Dudgeon, S.R. (1999). Experimental evidence for the origin of alternative communities on rocky intertidal shores. *Oikos*, **84**: 239–245.

Petraitis, P.S. & Latham, R.E. (1999). The importance of scale in testing the origins of alternative community states. *Ecology*, **80**: 429–442.

Petraitis, P.S., Rhile, E.C. & Dudgeon, S. (2003). Survivorship of juvenile barnacles and mussels: spatial dependence and the origin of alternative communities. *J. Exp. Mar. Biol. Ecol.*, **293**: 217–236.

Pihl, L., Magnusson, G., Isaksson, I. & Wallentinus, I. (1996). Distribution and growth dynamics of ephemeral macroalgae in shallow bays in the Swedish west coast. *J. Sea Res.*, **35**: 169–180.

Råberg, S., Jönsson, R.B., Björn, A., Granéli, E. & Kautsky, L. (2005). Effects of *Pilayella littoralis* on *Fucus vesiculosus* recruitment. Implications for community composition. *Mar. Ecol. Prog. Ser.*, **289**: 131–139.

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

Seymour, R.J., Tegner, M.J., Dayton, P.K. & Parnell, P.E. (1989). Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuar. Coast. Shelf Sci.*, **28**: 277–292.

Speidel, M., Harley, C.D.G. & Wonham, M.J. (2001). Recovery of the brown alga *Fucus gardneri* following a range of removal intensities. *Aquat. Bot.*, **71**: 273–280.

Thomsen, M.S. & Wernberg, T. (1995). Spatial distribution and abundance of macroalgae in the sublittoral zone of Bornholm – with reference to potential uses. M.Sc. thesis, Department of Geography and International Development Studies. Roskilde University.

Toohey, B., Kendrick, G.A., Wernberg, T., Phillips, J.C., Malkin, S. & Prince, J. (2004). The effects of light and thallus scour from *Ecklonia radiata* canopy on an associated foliose algal assemblage: the importance of photoacclimation. *Mar. Biol.*, **144**: 1019–1027.

Viejo, R.M., Aberg, P., Cervin, G. & Lindegarth, M. (1999). The interactive effects of adult canopy, germling density and grazing on germling survival of the rockweed *Ascophyllum nodosum*. *Mar. Ecol. Prog. Ser.*, **187**: 113–120.

Voipio, A. (1981). *The Baltic Sea*. Elsevier/North-Holland, Amsterdam.

Worm, B. & Chapman, A.R.O. (1998). Relative effects of elevated grazing pressure and competition from a red algal turf on two post-settlement stages of *Fucus evanescens* C. Ag. *J. Exp. Mar. Biol. Ecol.*, **220**: 247–268.

Worm, B., Lotze, H.K. & Sommer, U. (2001). Algal propagule banks modify competition, consumer and resource control on Baltic rocky shores. *Oecologia*, **128**: 281–293.