Geographic consistencies of effects of experimental physical disturbance on understorey species in sublittoral kelp forests in central New South Wales

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Abstract: Experimental physical disturbances on the assemblages of understorey species living in sublittoral kelp forests in central New South Wales were examined across several spatial and temporal scales. Experimental clearing of kelp canopies (mimicking damage done during storms) and subsequent macro- and microscopic sampling of cleared areas, edges of clearings and uncleared, control areas of natural kelp forest were done over a 14-month period across several spatial scales; three replicate patches of clearings and controls (3–5 m apart) in each of two sites (10–20 m apart) in each of two kelp forests (0.2–5 km apart) in each of four locations (20–140 km apart). Despite large variations in abundances and temporal fluctuations, there were some similarities in responses to disturbance by several taxa in most locations. The covers of holdfasts of Ecklonia radiata and encrusting algae decreased in the centres of most clearings in most kelp forests as plots became overgrown, first by microscopic filamentous algae and then by macroscopic foliose algae. While these changes occurred, a layer of sediment increased in cover in clearings and the species richness of the assemblage declined. Assemblages on the edges of clearings often showed effects intermediate between those in the centres of clearings and those under the natural canopy. In some forests, juveniles of Ecklonia radiata recruited, but this tended to occur toward the edges of clearings where the covers of microalgae, turf and sediment were least. The presence of turfing species in the centres of clearings also seemed to preclude the successful establishment of some sponges and an ascidian during their periods of recruitment. The microscopic and turfing algae which colonized clearings were different in different places, as were the periods after clearing before they colonized. Species that were fairly uniform in their responses to disturbance were common, occurring in similar abundances in most places. Temporal variability showed that some fluctuations occurred over a matter of weeks (e.g. the microscopic organisms), others occurred over several months (foliose algae), whilst the largest time-scale involved the recovery of the disturbed kelp canopy over the full duration of the experiment. Despite significant small-scale spatial patchiness in the responses of taxa to disturbances, these effects were fairly consistent within a particular forest. The results are discussed in terms of current theories of patch dynamics, as they apply to our understanding of kelp systems.

Key words: Canopy; Clearance; Experiment; Kelp forest; Spatial variability; Understorey

INTRODUCTION

Spatial and temporal variations in recruitment, immigration, emigration, mortality and rates of growth of species provide the basic ingredients of the assemblage of species

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in any locality. Physical processes and biological interactions act on these ingredients to determine the structure of the local assemblage at any place and time. Consideration of the natural regimes of spatial and temporal variability in an assemblage and how this variability affects the outcomes of physical and biological processes is therefore vital to identifying the most important factors determining its structure (Dayton et al., 1992 and reviews by Underwood & Denley, 1984; Connell & Keough, 1985). Recent reviews dealing with determinants of structure in intertidal and subtidal macroalgal assemblages have all noted, however, that there has been no single experimental study which examined interactions across broad spatial and temporal scales in kelp forests (Chapman & Johnson, 1990; Foster, 1990; Santelices, 1990; Schiel, 1990; Underwood & Kennelly, 1990).

In one of the few attempts to examine interactions over a wide area, Foster & Schiel (1990) sought to determine the geographic generality of specific interactions that have been identified as important in structuring the well-studied kelp forests of California. Using data from many surveys, these authors examined the well-known interaction between sea-otters, sea urchins and kelp (Estes & Palmisano, 1974; Dayton, 1975; Duggins, 1980). They concluded that generalities about these processes were unlikely to be valid because there had been no multi-factorial, multi-site study to determine the relative contributions of various interactions. They concluded that, to assess the geographical applicability of such interactions, replication must at least encompass the range of variability among sites in the region of interest.

In an ancillary paper (Kennelly & Underwood, 1992), we provided estimates of natural variability associated with the abundances of understorey species across several spatial scales in the kelp (Ecklonia radiata) forests of central New South Wales. In the present paper, we go a step further by experimentally assessing the geographic generality of a particular process which has been documented for one such kelp forest. This process concerns the effects on understorey species due to the physical disturbance of clearing kelp canopies (mimicking damage due to storms) and has been examined intensively in one location, Fairlight Bay, Port Jackson (Kennelly, 1987a,b). Clearing kelps in any season except winter led to encrusting algae, sponges and ascidians being overgrown first by filamentous algae, then by turfing algae. These algae then occupied the clearings for up to 14 months until individual kelps gradually re-invaded from the edges of experimental plots. In winter, however, juvenile kelps quickly colonized the substratum, leading to the rapid re-establishment of a canopy within 3–4 months. Partial denudation of kelp plants led to similar effects on most understorey species as those seen in areas where the canopy was completely removed, because the damaged kelps invariably died. Further, understorey assemblages on the borders of clearings contained a mixture of species normally found under the canopy and some species found in the centres of clearings. These previous studies showed that the type of assemblage in any place, at any time, depended on the timing of and time since the last removal of kelp. Other papers investigated these interactions in more detail, suggesting (1) a mechanism for the inhibition of kelp recruitment by turfing species in
clearings (Kennelly, 1987c); and (2) the mechanisms of removal of shade and changes in scouring that cause the responses to removal of kelp canopy (Kennelly, 1989).

To determine the geographic generality of these interactions, it was necessary to compare experimental clearances of canopies and uncleared controls across several spatial scales (Foster, 1990; Underwood & Kennelly, 1990). We do this in the present paper by examining effects of clearances at spatial scales ranging from less than 2 m up to 140 km throughout the central coast of New South Wales.

**Materials and Methods**

The locations of the kelp forests used in this experiment are given in Fig. 1 in Kennelly & Underwood (1992). They range over 350 km of coastline from Anna Bay in the north, to Jervis Bay in the south. All forests sampled were in sheltered bays, protected from all but extreme swells, at depths of 3 to 10 m. Densities of adult *E. radiata* (see below) ranged from 10 to 30/m², as reflected in the percentage covers of holdfasts described later. These forests differ in the numbers and types of species present, although some species were common at all places. The understorey assemblages in these forests contained encrusting algae, sponges, bryozoans, ascidians, brown, red and green algae, large mobile invertebrates (sea-urchins, turbinids, limpets) and many species of fish. The predominant understorey species were encrusting algae and sponges. Upon closer examination using an underwater microscope (Kennelly & Underwood, 1984), the benthic assemblages also included diatoms, blue-green and other filamentous algae, juveniles of larger plants (including kelp) and microscopic animals (ostracods, amphipods, gastropods, pedicellinids). The species found in one of these kelp forests were listed by Kennelly (1987b; Table 2). Fine detritus, silt and sand were also found amongst these organisms.

The largest spatial scale of sampling in the present experiments used four locations, spaced 20–140 km apart (Table I). At each location, two kelp forests, one north and one south, were sampled (spaced 0.2–5 km apart). This provides replication to demonstrate that differences found amongst locations were not due to confounded differences among forests closer together than the spatial scale of locations. In each forest, two sites (randomly spaced 10–20 m apart) were used for experimental treatments. Thus, differences among locations, forests and sites could unambiguously identify patterns at scales of 10’s of kilometres (locations), 100’s of metres to kilometres (forests) and 10’s of metres (sites).

In each site, three replicate patches were sampled (randomly spaced 3–5 m apart). In each patch in March 1986, a 2 × 2 m area of the natural kelp canopy was cleared of all kelp by cutting off stipes immediately above the holdfasts. Kennelly (1987b) showed that there were no effects on the understorey assemblage due to this form of clearance (other than the removal of the canopy) because no bare rock is exposed nor any holdfast infauna disturbed. This size of clearing was used because previous work
(Kennelly, 1987a,b,c; Kennelly, 1989) showed that it excluded any effects of the surrounding canopy from the central (1 × 1 m) portion of the clearing. Second, the edges of these 2 × 2 m clearings were sampled separately, i.e. that part of the clearing outside the central 1 × 1 m. Third, we established replicate undisturbed areas of natural kelp forest near each clearing. There may be some non-independence between the cleared and edge treatments because these were sampled in the same patches, but this has been ignored in the analyses. Each experimental treatment was sampled by independently-placed quadrats at each time of sampling, as described below. Replicate numbers and spacings of replicated quadrats, patches and sites were determined from the earlier work and the results of Kennelly & Underwood (1984) using the same sampling techniques.

Two methods were used to sample benthic assemblages. Three replicate 30 × 30 cm, 100-point quadrats were sampled in each experimental plot using the point-intersect method to estimate primary cover of all macroscopic benthic species. Any species forming a canopy were moved aside to estimate primary cover below them. Sand lying over organisms was not disturbed because this would reduce visibility. The numbers of juvenile E. radiata plants (less than 100 mm) and large mobile animals in each quadrat were recorded as the number per 0.09 m². When E. radiata recruits had grown larger than 100 mm, they were recorded as percent covers of holdfasts. The total number of species recorded in each quadrat was used to estimate the species richness of assemblages.

Microscopic organisms in each experimental plot were sampled in eight replicate fields of view (determined from pilot studies in Kennelly & Underwood, 1984) of an underwater microscope at a magnification of 53 × (each field of view covered 5 × 5 mm of substratum). A 9-point grid was used in the microscope to determine covers of

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**Table I**

Spatial scales investigated in experimental clearings; there were three treatments (cleared, edge and control, see text) in replicate patches, which were sub-sampled by quadrats to estimate abundances of macro- or microscopic species.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Distances apart</th>
<th>Details of replication</th>
</tr>
</thead>
<tbody>
<tr>
<td>Locations along coast</td>
<td>10s–100s km</td>
<td>Anna Bay, Port Jackson, Botany Bay, Jervis Bay</td>
</tr>
<tr>
<td>Forests in each location</td>
<td>0.2–5 km</td>
<td>Two forests (north and south) in each location</td>
</tr>
<tr>
<td>Sites in each forest</td>
<td>10–20 m</td>
<td>Two randomly-chosen sites in each forest</td>
</tr>
<tr>
<td>Replicate patches in each site</td>
<td>3–5 m</td>
<td>Three patches (2 × 2 m) with cleared and edge treatments; three control patches in each site</td>
</tr>
<tr>
<td>Quadrats</td>
<td>Within 2 × 2 m patches</td>
<td>Three quadrats (30 × 30 cm) for macroscopic species; eight fields of view for microscopic species</td>
</tr>
</tbody>
</table>
microscopic organisms. Data for sessile microscopic species were recorded as the relative cover (out of a maximum of 9 points) and microscopic animals were recorded as the total number of each species in each field of view.

Macroscopic and microscopic organisms were identified as accurately as possible in the field. Where necessary, samples were collected for further identification in the laboratory. All data were recorded on an underwater tape-recording system. Sampling was done 9 times throughout a 14-month period using macroscopic sampling and 5 times throughout a 13-week period using microscopic sampling. After 5 months, sampling was abandoned in one of the four locations (Botany Bay) because of a great inundation of freshwater which destroyed both kelp forests (Andrew, 1991).

Analyses of variance examined sources of variability across all spatial scales and experimental manipulations. Data for the major taxa were analysed for each of the first five sampling periods, after which the destruction of both forests in Botany Bay precluded the use of this analysis. Sets of data for all taxa were also analysed within each forest at each time of sampling using the relevant 3-factor analysis of variance. Cochran's tests for homogeneity of variances and (where appropriate) transformations were used prior to all analyses of variance. Sets of data which showed significant effects or interactions due to the experimental manipulations are presented in the graphs below.

**Results**

*Numbers of macroscopic species*

We present the results of the analyses of variance for this set of data in Table II as an example of the analyses done for all taxa. To conserve space, similar tables for other taxa are not included. There was little effect of removal of the canopy on the numbers of understorey species. There was no significant effect in forests in Anna Bay and Botany Bay (Fig. 1a,b,c). There was a significant interaction between clearing treatment and time of sampling in one forest in Anna Bay, due to the fluctuations from time to time in the numbers of species in different treatments (Fig. 1a). Similar fluctuations in the other forest and in Botany Bay (Fig. 1b,c) were not significant.

In the other locations, numbers of species in edges were always similar to controls, but there was a sustained reduction in the clearings (Fig. 1c,d,e,f). In all four forests, the number of species declined within 2 weeks after the start of the experiment, but in the northern forests of Port Jackson and Jervis Bay there were also similar downward trends in the edge and control treatments at the beginning of the experiment (Fig. 1c,g). Thus, significant differences from the cleared treatments became apparent somewhat later. The reduction in number of species was greater in Jervis Bay than elsewhere (Fig. 1g,h). Note, however, that the removal of canopy caused a decrease in mean number of less than one species per quadrat.
TABLE II

Analyses of variance for the numbers of species recorded in each kelp forest throughout the experiment. ** indicates significance, \( p < 0.01 \); *, \( p < 0.05 \). Data were available from Botany Bay for the first six sampling periods; the temporal degrees of freedom for forests in Botany Bay were: Time, 5; T x S, 5; T x P (S), 20; T x C, 10; T x C x S, 10; T x C x P (S), 40; Residual, 216.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Anna Bay</th>
<th>Port Jackson</th>
<th>Botany Bay</th>
<th>Jervis Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>North</td>
<td>South</td>
<td>North</td>
<td>South</td>
</tr>
<tr>
<td></td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Time</td>
<td>8</td>
<td>15.43 6.16**</td>
<td>14.55 4.15*</td>
<td>16.75 7.59**</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>39.19 6.9</td>
<td>0.53 0.23</td>
<td>0.21 0.06</td>
</tr>
<tr>
<td>Patch (Site)</td>
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<td>5.68 3.70**</td>
<td>2.27 1.56</td>
<td>3.40 2.25</td>
</tr>
<tr>
<td>Clearing treatment</td>
<td>2</td>
<td>1.62 0.66</td>
<td>0.39 2.08</td>
<td>32.25 2.47</td>
</tr>
<tr>
<td>T x S</td>
<td>8</td>
<td>2.50 0.83</td>
<td>3.50 1.55</td>
<td>2.21 1.43</td>
</tr>
<tr>
<td>T x P (S)</td>
<td>32</td>
<td>3.04 1.98**</td>
<td>2.25 1.54*</td>
<td>1.54 1.07</td>
</tr>
<tr>
<td>T x C</td>
<td>16</td>
<td>4.39 2.56*</td>
<td>1.69 0.82</td>
<td>3.13 1.41</td>
</tr>
<tr>
<td>C x S</td>
<td>2</td>
<td>2.46 0.75</td>
<td>0.19 0.12</td>
<td>13.06 4.01</td>
</tr>
<tr>
<td>C x P (S)</td>
<td>8</td>
<td>3.30 2.15*</td>
<td>1.58 1.08</td>
<td>3.26 2.16*</td>
</tr>
<tr>
<td>T x C x S</td>
<td>16</td>
<td>1.71 0.87</td>
<td>2.07 1.24</td>
<td>2.22 1.20</td>
</tr>
<tr>
<td>T x C x P (S)</td>
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<td>1.98 1.29</td>
<td>1.67 1.15</td>
<td>1.86 1.73</td>
</tr>
<tr>
<td>Residual</td>
<td>324</td>
<td>1.53 1.46</td>
<td>1.51 1.35</td>
<td>1.40 1.26</td>
</tr>
</tbody>
</table>
Fig. 1. Mean (± SE; n = 18) number of macroscopic species in kelp forests in Anna Bay north (a), south (b); Port Jackson north (c), south (d); Botany Bay north (e), south (f); Jervis Bay north (g), south (h). In this and subsequent Figures, —— is cleared centres of patches, - - - is edges of cleared patches and ● ● ● is untouched controls. No data were collected in Botany Bay after July, 1986 (see text). Experimental patches were cleared of kelp in March, 1986 after the first time of sampling shown in the Figure.
Effects on *Ecklonia radiata*

The percentage covers of holdfasts of the kelp, *E. radiata*, provided estimates of abundances of large plants (> 100 mm). In all forests, these covers decreased in experimentally cleared areas (Fig. 2) as the holdfasts became overgrown by other species.

Fig. 2. Mean (± SE; n = 18) percentage cover of holdfasts of the kelp, *E. radiata*, in Anna Bay north (a), south (b); Port Jackson north (c), south (d); Botany Bay north (e), south (f); Jervis Bay north (g), south (h).

*Time of Sampling*
(see below). After about 6 months, there was little or no cover of holdfasts of large plants, but there was some slight recovery by the end of the experiment.

There were declines in cover of *E. radiata* on the edges of clearings in all forests except those in Anna Bay (Fig. 2a,b) and greater recovery, in many cases back to control abundances by the end of the experiment.

Juvenile *E. radiata* recruited in some numbers in the forests in Port Jackson and Jervis Bay (Fig. 3) leading to short-term increases in cover in those forests. In both forests in Port Jackson, *E. radiata* recruited only to the edges of clearings (Fig. 3a,b). In the northern forest of Jervis Bay, recruitment was much greater on the edges than in control or cleared areas (Fig. 3c). In contrast, in the southern forest of Jervis Bay, kelps recruited to control (uncleared) and edge treatments (Fig. 3d). The recruits only persisted for a few months where they occurred, because they then had grown large enough to be considered as large plants (see Methods) and were included in estimates of percentage covers of holdfasts. Small numbers of *E. radiata* recruited into experimental patches in the north site at Anna Bay, leading to a small, but non-significant increase in cover of holdfasts (as in Fig. 2a).

*Understorey foliose algae*

The dictyotalean turfing algal complex, *Zonaria Lobophora*, increased in cover in clearings compared to control areas in most kelp forests (Fig. 4). The growth of

![Graph](image-url)
Fig. 4. Mean (± SE; n = 18) percentage cover of the brown algal complex, *Zonaria*/Lobophora in Anna Bay north (a), south (b); Port Jackson north (c), south (d); Botany Bay north (e), south (f); Jervis Bay north (g), south (h).

*Zonaria*/Lobophora on the edges of experimental clearings differed greatly among kelp forests, in magnitude of change and in the pattern shown among treatments.

In the northern forest in Port Jackson and in the southern forest in Jervis Bay, these algae increased on edges in a similar fashion to the increases in the centres of clear-
ings (Fig. 4c,h). In the northern forest in Anna Bay and the southern forest in Botany Bay, covers of *Zonaria/Lobophora* on the edges of clearings resembled those in control areas and were less than those in cleared treatments (Fig. 4a,f). This was also the case in the southern forest in Anna Bay, after an early increase in cover in the edges (Fig. 4b). Yet other forests – the southern forest in Port Jackson and the northern one in Jervis Bay – had an increased cover of *Zonaria/Lobophora* in the edges of experimental plots, but not as great a cover as that developed in the centres of clearings (Fig. 4d,g).

The effects of experimental clearing of kelps on the fucalean algae, *Sargassum* spp., were also very variable from place to place. In the northern forest in Port Jackson and the southern forest in Jervis Bay, cover of *Sargassum* spp. increased in the centres of clearings whilst remaining small on the edges of clearings and in control areas (Fig. 5a,d). In the southern forest in Port Jackson and the northern forest in Jervis Bay, covers of *Sargassum* spp. increased in the centres and on the edges of experimental patches (Fig. 5b,c).

There were several other significant changes in covers of foliose understorey species in different forests and, for the most part, represented very small increases in mean percentage covers. For example, the dictyotalean alga, *Padina fragile*, increased to a mean cover of $\approx 10\%$ of the surface in the centres of clearings in the northern forest in Port Jackson, with a rapid decrease occurring toward the end of sampling (Fig. 6).
In Botany Bay, the green turfing alga, *Ulva lactuca*, increased (by less than 3%) in the centres of clearings, slightly increased on the edges but did not change in control areas. The red turfing alga, *Wrangelia plumosa*, appeared in the northern forest in Botany Bay, but only in the centres of cleared plots. It was not seen in other forests. The data for these latter species are not presented (to save space).

**Understorey encrusting algae**

The encrusting alga, *Neogoniolithon* sp., showed a marked decrease in the centres of clearings and, usually, a smaller decrease in the edges of clearings (Fig. 7). This occurred in all kelp forests sampled. Similar effects occurred for other encrusting algae, the *Peyssonelia/Hildenbrandia* complex, in the northern forest in Anna Bay and in both forests in Port Jackson (Fig. 8a,c,d). There were no significant differences in cover of *Peyssonelia/Hildenbrandia* in other forests. For *Neogoniolithon* sp. and *Peyssonelia/Hildenbrandia*, the cover in experimentally cleared plots had virtually converged to control levels by the end of the experiment.

**Encrusting animals**

In both forests in Port Jackson, the encrusting sponge, *Tedania connectans*, showed an increase in control areas but no increase on the edges nor in the centres of clearings (Fig. 9a,b), although these increases were not at the same time in the two forests. By the end of the experiment, covers of *T. connectans* had reduced to be similar to the

![Graph](image_url)

*Fig. 6. Mean (± SE; n=18) percentage cover of Padina fragile in Port Jackson north.*
covers in edge and cleared treatments. In the northern forest in Port Jackson, the colonial ascidian *Didemnum moseleyi* increased in control areas and, to a lesser extent, on the edges of clearings (Fig. 9c). A slower increase in cover in the cleared treatments and a decline in the other treatments resulted in similar covers by the end of the ex-
Fig. 8. Mean (± SE; n = 18) percentage cover of the encrusting red algal complex, *Peyssonelia/Hildenbrandia*, in Anna Bay north (a), south (b); Port Jackson north (c), south (d); Botany Bay north (e), south (f); Jervis Bay north (g), south (h).

The sponge, *Callyspongia romosa*, showed a short-term increase in cover in the control areas of the northern forest in Jervis Bay (Fig. 9d), but then declined to its original mean cover.
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Fig. 9. Mean (+ SE; n = 18) percentage cover of the sponge, *Tedania connectans*, in Port Jackson north (a), south (b); *Didemnum moseleyi* in Port Jackson north (c); and *Callyspongia ramosa* in Jervis Bay north (d).

Sediments

A layer of fine sediment (an inextricable mixture of fine silt, unicellular, filamentous algae and micro-invertebrates) underwent large increases in the centres of clearings in most kelp forests, but this was only short-lived – decreasing to control levels within a few months (Fig. 10). On the edges of clearings, this increase was only slight and, in most cases, not significantly different from control areas.

A few months after the start of the experiment, the cover of sand (coarser particles, easily distinguished from the layer of sediment mentioned above) increased in clearings in most forests (Fig. 11). The increase was greater in the centres than on the edges of clearings. Generally, cover of sand decreased again toward the end of sampling to control levels, except in the southern forest in Jervis Bay, where control levels of sand increased to the levels found in clearings. In the northern forest in Port Jackson and the southern forest in Botany Bay, removal of kelp had no significant effect on the cover of sand (Fig. 11c,f).

The general pattern was for sand to increase in cover in forests after the cover of the sediment layer declined (compare Figs. 10 and 11).

Microscopic sampling

Of the taxa sampled with the underwater microscope, four showed significant effects due to clearing the kelp canopy. In most forests, the filamentous green alga, *Entero-
Fig. 10. Mean (±se; n = 18) percentage cover of fine silt in Anna Bay north (a), south (b); Port Jackson north (c), south (d); Botany Bay north (e), south (f); Jervis Bay north (g), south (h).

*orpha intestinalis* showed large increases in the centres of clearings just two weeks after clearing (Fig. 12). These large covers then declined to natural levels in some forests (Anna Bay south and both forests in Botany Bay; Fig. 12b,e,f). In other forests, covers remained greater than controls throughout the period of sampling (after 13 weeks; Fig. 12a,c,d,g,h). Microscopic covers of *E. intestinalis* on edges
of clearings were intermediate between those in the centres and those in control areas.

In all forests (except those in Jervis Bay), the filamentous ectocarpalean alga, *Giffordia mitchelliae*, showed large and usually immediate increases in the centres of clearings with large decreases occurring soon after (Fig. 13). On edges of clearings, increases in cover were smaller, whilst no significant changes occurred in control plots.
DISCUSSION

The concept of patch dynamics has been a popular topic in recent reviews and discussions of the ecology of kelp systems (Foster, 1982; Foster & Schiel, 1985;
Fig 13 Mean (± SE; n = 48) relative cover of the microscopically sampled brown alga, *Giffordia mitchelli*ae in Anna Bay north (a), south (b); Port Jackson north (c), south (d); Botany Bay north (e), south (f); Jervis Bay north (g), south (h).

Dayton, 1985; Dayton et al., 1992, see reviews in Chapman & Underwood, 1990). In discussing this concept, kelp ecologists usually mean those mechanisms which determine the assemblage of species in a given place and the processes causing this to vary from place to place and time to time. Unfortunately, whilst many authors discuss
these ideas, few have attempted to quantify these mechanisms and so describe the dynamics of individual kelp systems (see also Foster, 1990). By the nature of any definition of “patch dynamics”, the experimental investigation of the mechanism in question must encompass spatial and temporal scales which are appropriate for the particular system under examination. That is, the location (in space and time) of the “patches” the “dynamics” of which are being investigated must be adequately defined and included in experimental designs. As discussed by Schiel (1990), Underwood and Kennelly (1990) and, most notably, Foster (1990), the lack of such information is currently the single largest shortfall in our understanding of kelp systems throughout the world.

In central New South Wales, previous work on the patch dynamics of kelp assemblages provided some information about effects of the physical disturbance of removing kelp canopies on the assemblages of organisms living in one kelp forest in Port Jackson (Kennelly, 1987a–c; 1989). The experimental design used in the present study allowed us to determine the relevance of these processes to kelp forests over a much wider spatial scale. Effects similar to those documented in the previous papers were in evidence in most kelp forests examined, although the specific nature of these interactions was not consistent everywhere. As found previously (Kennelly, 1987b), the covers of holdfasts of *E. radiata* and encrusting algae (*Neogoniolithon* sp. and *Peyssonelia/Hildenbrandia* complex) decreased in the centres of most clearings in most kelp forests as plots became overgrown firstly by microscopic filamentous algae (*Enteromorpha intestinalis, Giffordia mitchelliae*) (Figs 2, 7, 8, 12 and 13). After a few months, macroscopic foliose algae (*Zonaria/Lobophora* complex, *Sargassum* spp., and lesser amounts of *Padina fraseri, Ulva lactuca* and *Wrangelia plumosa*) replaced these filamentous forms as the dominant occupier of space in clearings (Figs 4–6). Whilst these changes occurred, a layer of sediment increased in cover in clearings (Fig. 10) and the species richness of the assemblage declined in some forests (Fig. 1). Further, as was the case in Kennelly (1987b), assemblages on the edges of clearings in the present study often showed effects intermediate between those in the centres of clearings and under the natural canopy.

These experiments were not designed to test hypotheses about specific processes causing patterns of occupation of cleared patches. Nevertheless, they provide an opportunity to consider the generality of processes previously found to be important in experimental studies at one or a few locations.

The patterns observed conform well with the interpretations of Kennelly’s (1987a–c) experiments. Opportunistic microscopic filamentous algae seems to occupy space soon after disturbances but are subsequently replaced by the slower-growing but larger foliose species (Kennelly, 1987a–c). As found by Kennelly (1989), these patterns were probably a result of an increase in the light regime following the removal of the canopy. The presence of the larger thalli may then have been responsible for the greater entrapment and corresponding increase in cover of sediment. As this sediment and foliose algae increased in cover, the more opportunistic species declined, bringing about
an overall decrease in the species richness of the assemblage. It is, however, necessary for more widespread experimental studies to test hypotheses derived from this general model.

In some forests, juveniles of *E. radiata* recruited, but this tended to occur toward the edges of clearings where the covers of micro-algae, turf and sediment were least (Fig. 3). As was the case previously (Kennelly, 1987c), the presence of turfing species in the centres of clearings seemed to preclude the successful establishment of kelps during their period of recruitment. Such inhibition was also evident as covers of the sponges *Tedania connectans* and *Callyspongia romosa* and of the ascidian *Didemnum moseleyi* increased in control areas in some kelp forests, but did not increase in clearings where a turfing assemblage dominated (Fig. 9).

Whilst many of these changes in structure are similar to those documented previously for a single kelp forest, not all clearings in all forests displayed these effects. In particular, the identity of the microscopic and turfing algae which colonized these clearings was different in different places, as were the lengths of time after clearing when colonizations occurred. For example, *Zonaria/Lobophora* complex formed a dominant turfing cover in experimental clearings in most forests despite its small cover under natural canopies. The increased cover, however, occurred after 10 weeks in some forests, after 20 weeks in others and not at all in one of the eight forests sampled (Fig. 4). Such was the case for most taxa, leading us to conclude that the identity of understory species affected by physical disturbances in kelp forests depends on the availability of such species to colonize patches within a particular forest at any particular time. Foster (1975) in one of the first experimental studies of succession in kelp forests drew similar conclusions about the timing and seasonality of events affecting different species.

Thus, while the structure and dynamics occurring within these various forests are reasonably similar everywhere, the mixture of species and timing of changes are not necessarily similar from one forest to another. Therefore, if the object of the quantification of patch dynamics is to describe such systems properly, then the focus must be at a species-specific level - not at the scale of communities, "sea-scapes" or habitat-types. Such broader categorizations must obscure the species-specific and small-scale temporal variability which are a major and presumably important feature of these systems.

Those species which were fairly uniform in their responses to disturbance (*Neogoniolithon* sp., *Peyssonelia/Hildenbrandia* complex, *Enteromorpha intestinalis*, differ from those which were more place-specific in their responses (*Padina fraseri*, the sponges) in that they were more common, occurring in similar abundances in most places. The latter species were only present in sufficient abundances to be influenced by disturbance in certain places. The obvious, almost trivial conclusion to be gained from this is that such species cannot be influenced by disturbances over a wide geographical range because they simply do not occur throughout the range.

The various types of temporal variability evident in this paper showed that some
The numbers of kelp forests which showed significant differences ($p < 0.05$) in the sources of variation in analyses of variance of the seven major sets of data. N.B. For all sets of data, the total number of forests considered was eight except for the percentage cover of *Zonaria/Lobophora* which only occurred in six forests.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Number of species</th>
<th>% cover of <em>Ecklonia</em> holdfasts</th>
<th>% cover of <em>Neogoniolithon</em></th>
<th>% cover of <em>Peyssonelia/Hildenbrandia</em></th>
<th>% cover of sand</th>
<th>Relative cover of <em>Enteromorpha</em></th>
<th>% cover of <em>Zonaria/Lobophora</em></th>
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<tbody>
<tr>
<td>Time</td>
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<td>5</td>
<td>4</td>
<td>7</td>
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<td>5</td>
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<td>0</td>
<td>3</td>
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<td>1</td>
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<tr>
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<td>6</td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>5</td>
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<tr>
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<td>6</td>
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</table>
fluctuations occurred over a matter of weeks (e.g. microscopic organisms), others occurred over several months (foliose algae), whilst the largest time-scale involved the recovery of the disturbed kelp canopy (and the associated cover of holdfasts in some forests; Fig. 2) over the full duration of the experiment (14 months, a similar recovery time to that documented previously for one forest; Kennelly, 1987a). The conclusion from this is that such variation tends to follow the relative size and rates of growth of the taxa in question, with smaller, faster-growing taxa showing temporal variabilities over smaller time scales than larger, slower-growing taxa.

To examine sources of variability across several spatial scales in detail, it is useful to consider how consistent were differences in sources of variation at spatial scales within forests across the eight kelp forests sampled. This is done in Table III which contains a summary of results from the analyses of variance for the seven taxa common to most forests. It is interesting to note that the main effect of Site and those higher-order interactions involving Site showed significant differences in far fewer forests than those sources of variation involving Patches. That is, the numbers of forests in which Site, T × S, C × S and T × C × S were significant were smaller than those in which Patch, T × P, C × P and T × C × P were significant. This result implies that effects of physical disturbance and complicating effects of temporal variability occurring on effects of physical disturbance occur to a greater extent at the scale of patches (3–5 m apart) than at the scale of sites (10–20 m apart). Thus, despite significant small-scale patchiness in the response of taxa to disturbances, these effects are fairly consistent within a particular forest.

The experimental design and results discussed in this paper highlight the necessity for appropriate temporal and spatial scales to be included in assessing the geographic generality of interactions (see review in Underwood & Petraitis, 1992). Only through an extensive incorporation of such scales, can the dynamics of any assemblage be accurately described with respect to the mechanisms and processes that cause its observed structure.

ACKNOWLEDGEMENTS

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