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Physical disturbances in an Australian kelp community. II. Effects on understorey species due to differences in kelp cover

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ABSTRACT: Physical disturbances in a sublittoral kelp community were investigated for their roles in structuring benthic assemblages. Effects of storms that lead to partial and/or complete denudation of kelp plants were investigated in a series of manipulative field experiments. Effects on understorey species due to differential damage to kelp plants were examined by sampling replicate plots of treatments that imitated the various kinds of damage to kelps. Partial damage to kelp canopies led to similar effects on species to complete removal of kelps, because damaged plants invariably died. Encrusting algae and sponges decreased in cover in manipulated areas while microalgae and then brown turfing species increased in cover. Consequences of living on the borders of clearings in the kelp forest were investigated. Understorey assemblages here contained abundances of both those species found under the kelp canopy and those in the centres of clearings. Effects on understorey species due to thinning the kelp canopy to various densities was investigated. Thinning kelp canopies had similar effects for most species as complete removal of canopies. Fluctuations in abundances of certain species required the removal of at least 50 % of the kelp canopy. Effects on colonizing species of providing clean primary substrata under kelp canopies (as when kelp holdfasts are detached) were investigated. The identity of the various micro-algae that colonized areas of bare substrata under the canopy showed marked variability among replicate sites. Results illustrated several complex influences that physical disturbances have on the structure of a kelp community, and indicate the need for comprehensive experimental studies of the effects of physical disturbances.

INTRODUCTION

Physical disturbances affect the distributions and abundances of species living in many ecosystems (Pickett & White 1985). The frequency, severity and timing of physical disturbances determines which species are removed, the time of removal, and therefore the structure of the community in that place (Levin & Paine 1974, Sousa 1984, Connell & Keough 1985). In particular, physical disturbances have been noted to structure marine communities by renewing the limiting resource of space for the colonization of intertidal (e.g. Dayton 1971) and subtidal species (Connell & Keough 1985). In sublittoral kelp communities the main physical disturbances are due to storms and associated water turbulence. These dislodge kelps and have many subsequent effects on the assemblage of species in understorey communities (Rosenthal et al. 1974, Foster 1982, Dayton & Tegner 1984, Dayton et al. 1984, Santelices & Ojeda 1984, Ebling et al. 1985).

Despite the number of studies on the effects of canopy removal on kelp communities (see reviews by Dayton 1985, Foster & Schiel 1985), several aspects have been partially or totally ignored. First, the effects on understorey species of differential damage to kelp plants has rarely been examined. Not all plants may be totally removed by storms (as is the case in most experiments). For stipitate kelps, the fronds, the fronds and stipes, or whole plants may be removed. Second, storms may not tear out all plants in areas, but only thin the canopy by detaching a few plants (see also Dayton et al. 1984). Different densities of kelp canopies may affect understorey species in different ways. Third, the colonization of understorey species onto new primary substratum (made available by the removal of kelp holdfasts) has rarely been examined. Those species

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Table 1. Designs of experiments

Expt	Purpose	Treatments	Replication	Started	Duration
1	Effects of differential damage to kelp plants. Differences between middles and edges of clearings	Whole kelp; no kelp; holdfasts; holdfasts & stipes. Middles; edges of clearings	Four 2 × 2 m areas	Dec 1982	14 mo
2	Effects of thinning kelp canopy	Totally cleared; half cleared; quarter cleared; uncleared areas	Three 2 × 2 m areas	Apr 1984	3 mo
3	Effects of removal of holdfasts	Cleared to bare rock; uncleared areas	3 sites, each with four 75 × 75 mm areas	Apr 1985	14 wk

that colonize bare rock may differ from those that colonize areas of encrusting algae. Fourth, few studies have been made on the effects of living on the edges of clearings (Dayton & Oliver 1981, but see Jackson 1983). These influences may be important for recolonization into clearings following disturbance (Connell & Keough 1985).

The preceding article (Kennelly 1987) described the natural frequency and severity of effects of storms on a kelp population, and effects on the understorey community due to the removal of the canopy in different seasons. The present article describes the effects of several other aspects of physical disturbance in this community. Manipulative experiments were done which examine the effects on understorey species due to differential damage to kelp plants, removing different numbers of kelp plants, exposure of clean substratum following the removal of kelp holdfasts, and the consequences of living on the edges of clearings.

MATERIALS AND METHODS

The study site was 4 m below low-tide level in a kelp forest in Fairlight Bay, Port Jackson, Sydney, Australia (33° 48′ S; 151° 16.5′ E). A description of the kelp forest in this area may be found in Kennelly (1983) and Kennelly (1987). The kelp at Fairlight is the stipitate *Ecklonia radiata* (C. Agardh J. Agardh).

The understorey assemblage under the kelp canopy at Fairlight contains several types of encrusting algae, sponges, bryozoans, ascidians, and brown, red and green algae. Upon closer examination using an underwater microscope (Kennelly & Underwood 1984), these assemblages are seen to also include diatoms, blue-green and other filamentous algae, juveniles of larger plants (including kelp) and microscopic animals (ostracods, amphipods and gastropods). Fine detritus and silt are found amongst these organisms.

Earlier surveys (Kennelly 1987) showed that physical disturbances due to great water turbulence during storms affected the forest by dislodging whole plants, parts of plants and groups of plants. Effects of these disturbances were examined in the following manipulative experiments (Table 1).

Expt 1. Effects on understorey species due to differential damage to kelp plants, and effects of borders of clearings. Areas of the kelp forest were manipulated by (i) removing all the kelps in each patch; (ii) removing only the kelp fronds (leaving the stipes and holdfasts); (iii) removing the stipes and fronds (leaving the holdfasts); and (iv) leaving the kelp plants alone as a control. Areas of 2 × 2 m were used as this was found to be the most common size of natural clearances in the canopy at Fairlight. This was also the minimum size that allowed no shading of the centre of the clearing by the surrounding canopy. Four replicate areas were used for each treatment. To determine different effects in the middles and edges of clearings, the 4 patches of the 4 treatments were sampled on both the outer 0.3 m wide perimeter and the central 2 m^2 portion of each clearing.

Expt 2. Effects of removal of different densities of kelp plants. To determine effects on the understorey community, replicate 2 × 2 m areas were: (i) cleared of all kelp; (ii) had half the number of resident kelp plants removed at random; (iii) had one quarter of the resident kelp plants removed at random; and (iv) were left with all kelp present as a control.

Expt 3. Effects of detachment of kelp holdfasts and creation of clean substrata. When holdfasts are detached from the substratum, small (ca 75 × 75 mm) areas of clean sandstone are left. The establishment of species on such areas was estimated by microscopically sampling 75 × 75 mm areas of clean substratum under the natural kelp canopy (a hammer and chisel was used to expose clean sandstone). Control areas were similar-sized areas of natural substratum covered by encrusting species. Four such clearances (and corresponding controls) were set up in 3 randomly selected locations (Sites 1, 2 & 3) in the kelp forest.

Sampling. Sampling these experiments involved 2

Table 2. List of the species in the assemblage associated with the kelp community at Fairlight

- Cyanophyta
  - *Anacystis* sp.
  - *Oscillatoria* sp.
- Chlorophyta
  - *Licmophora* sp.
  - *Enteromorpha intestinalis* (Linnaeus) Link
  - *Enteromorpha clathrata* (Roth) J. Agardh
  - *Ulva lactuca* (Linnaeus)
  - *Codium lucassii* Setchell
  - *Codium fragile* (Suringer) Hariot
  - *Chaetomorpha aerea* (Dillwyn) Koetzing
- Phaeophyta
  - *Zonaria sinclairii* Hooker & Harvey
  - *Zonaria turneriana* J. Agardh
  - *Zonaria augustata* (Kuetzing) Papenfuss
  - *Ectocarpus fasciculatus* (Clayton)
  - *Giffordia mitchelliae* (Harvey)
  - *Ecklonia radiata* (C. Agardh) J. Agardh
  - *Sphacelaria* spp.
  - *Sargassum* spp.
  - *Dictyopteris muelleri* (Sonder)
  - *Lobophora variegata* (Lamouroux) Womersley
  - *Dilophus marginatus* J. Agardh
  - *Dictyota dichotoma* (Hudson) Lamouroux
  - *Dictyota furcellata* (C. Agardh) J. Agardh
  - *Colpomenia sinuosa* (Roth) Derbes & Solier
  - *Padina fraseri* (Greville)
- Rhodophyta
  - *Hildenbrandia prototypus* Nardo
  - *Peyssonelia gunniana* J. Agardh
  - *Neogoniolithon* sp.
  - *Rhodymenia* sp.
  - *Acrosorium* sp.
  - *Phycodrys* sp.
  - *Callithamnion* sp.
  - *Haliptilon officinalis* Lamouroux
  - *Amphiroa* sp.
  - *Jania* sp.
  - *Polysiphonia* spp.
  - *Champia compressa* Harvey
  - *Ceramium* sp.
  - *Delisea pulchra* (Grev.) Mont.
- Porifera
  - *Callyspongia* sp.
  - *Myxilla* sp.
  - *Psammocinia* sp.
  - *Axociella* sp.
  - *Aplysilla sulfurea* (Schulze)
  - *Suberites* sp.
  - *Aplysilla rosea* (Barrois)
- Bryozoa
  - *Gigantopora biturrita* (Hincks)
  - *Watersipora arcuata* (Banta)
  - *Conopeum tenuissimum* (Banta)
- Bryozoa (continued)
  - *Membranipora membranacea* (Linnaeus)
  - *Orthoscuticella* sp.
- Entoprocta
  - *Pedicellina* sp.
- Cnidaria
  - *Sertularia* sp.
  - *Aglaophenia* sp.
  - *Cnidopus verater* (Drayton)
- Annelida
  - *Sphaerosyllis* sp.
  - *Diopatra dentata* Kinberg
  - Several other species in the family Syllidae
- Echinodermata
  - *Centrostephanus rogersii* (Agassiz)
  - *Holopneustes pycnotilus* Clark
  - *Phyllacanthus parvispinus* Tenison-Woods
  - *Heliocidarus erithrogramme* (Valenciennes)
- Mollusca
  - *Turbo torquata* (Gmelin)
  - *Cronia pseudomydala* Hedley
  - *Patelloida alticostata* (Angas)
  - *Eatoniella galbina* Laseron
- Crustacea : Amphipoda
  - *Cypraidea ornata* Haswell
  - *Ericthonius* sp.
  - *Nelita* sp.
  - *Dulichiella* sp.
  - Ostracoda
    - *Skogsbergia curvata* Poulsen
    - *Bairdia* sp. 1
    - *Bairdia* sp. 2
    - *Xestolebris tegrina* (Brady)
    - *Xestolebris reniformis* (Brady)
  - Cirripedia
    - *Balanus amphitrite* Darwin
  - Several unidentified copepods
- Protozoa : Foraminifera
  - *Quinqueloculina subpolygona* (Parr)
  - *Oolina hexagona* (Williamson)
  - *Lammellodiscorbis dimidiatus* (Jones & Parker)
- Chordata : Ascidia
  - *Didemnum* sp.
  - *Pyura pachydermatina* (Herdman)
  - Pisces
    - *Atypichthyes strigatus* (Gunther)
    - *Pseudolabrus gymnogenus* (Gunther)
    - *Pictilabrus laticlavius* (Richardson)
    - *Scorpis lineolatus* Kner
    - *Acanthopagrus australis* (Owen)
    - *Chrysophrys auratus* (Bloch & Schneider)
    - *Meuschenia trachylepis* (Gunther)

techniques that included as many understorey organisms as possible. These techniques are described in Kennelly (1987). Macroscopic benthic organisms were sampled in all experiments using 3 randomly placed, 30 × 30 cm, 100-point quadrats to record percentage covers (using the point-intersect method). The relative abundances of microscopic organisms were determined using a 9-point quadrat in an underwater microscope (Kennelly & Underwood 1984) at a magnification of 53× (each field of view covered 5×5 mm of sub-

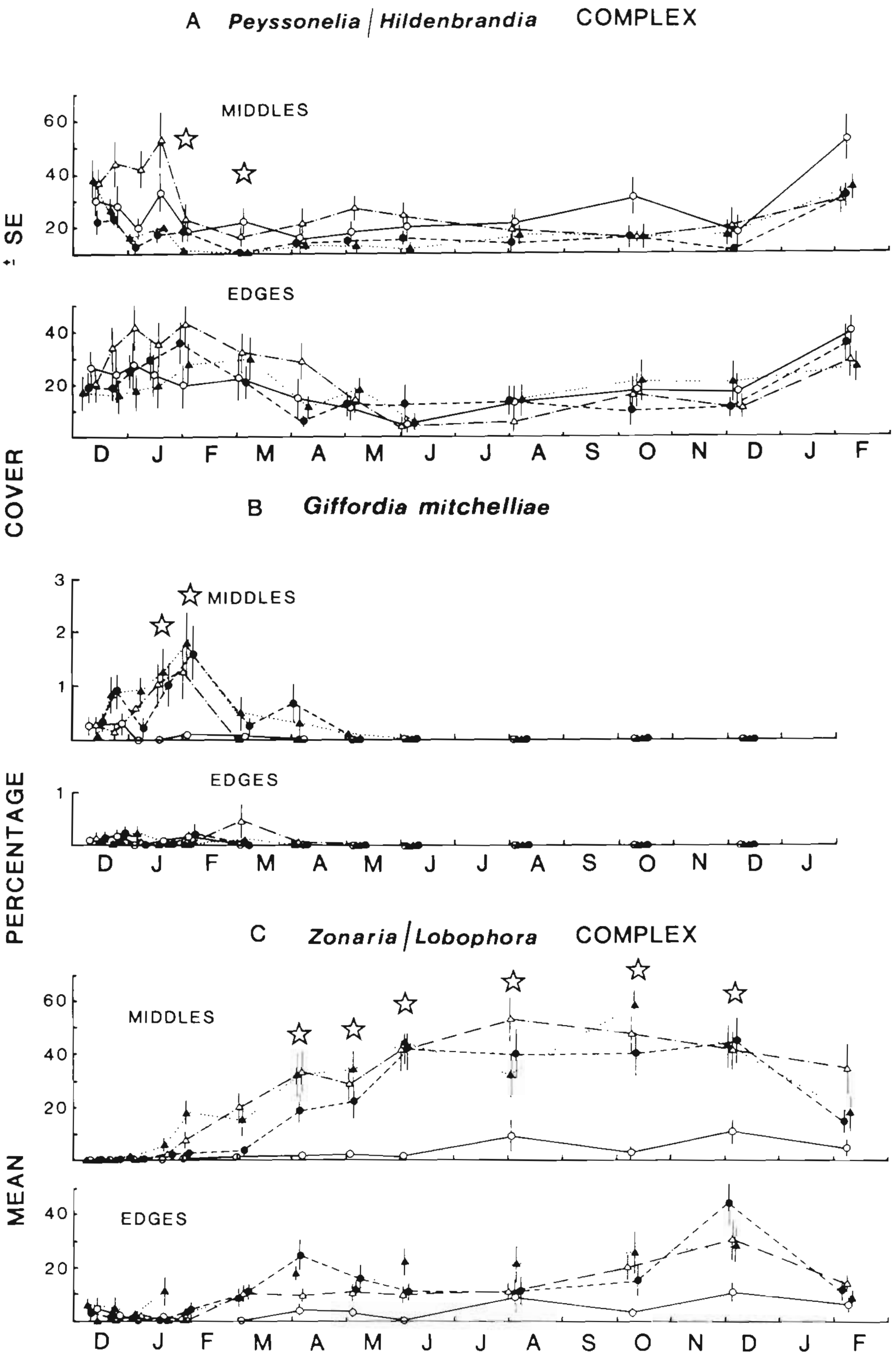

Fig. 1 Effects on the cover of (A) *Peyssonelia/Hildenbrandia* complex, (B) *Giffordia mitchelliae*, and (C) *Zonaria/Lobophora* complex due to differential damage to surrounding kelp plants *Ecklonia radiata*, in the middles and edges of experimental plots. Treatments were: (△) areas cleared of all kelp; (▲) areas cleared of only laminae and stipes of kelp; (●) areas cleared of only laminae of kelp; (○) areas of natural kelp canopy (n = 12). In this and subsequent figures, ☆ denotes a significant difference among the plotted means determined in the analysis of variance of the data and SNK comparisons at that time of sampling

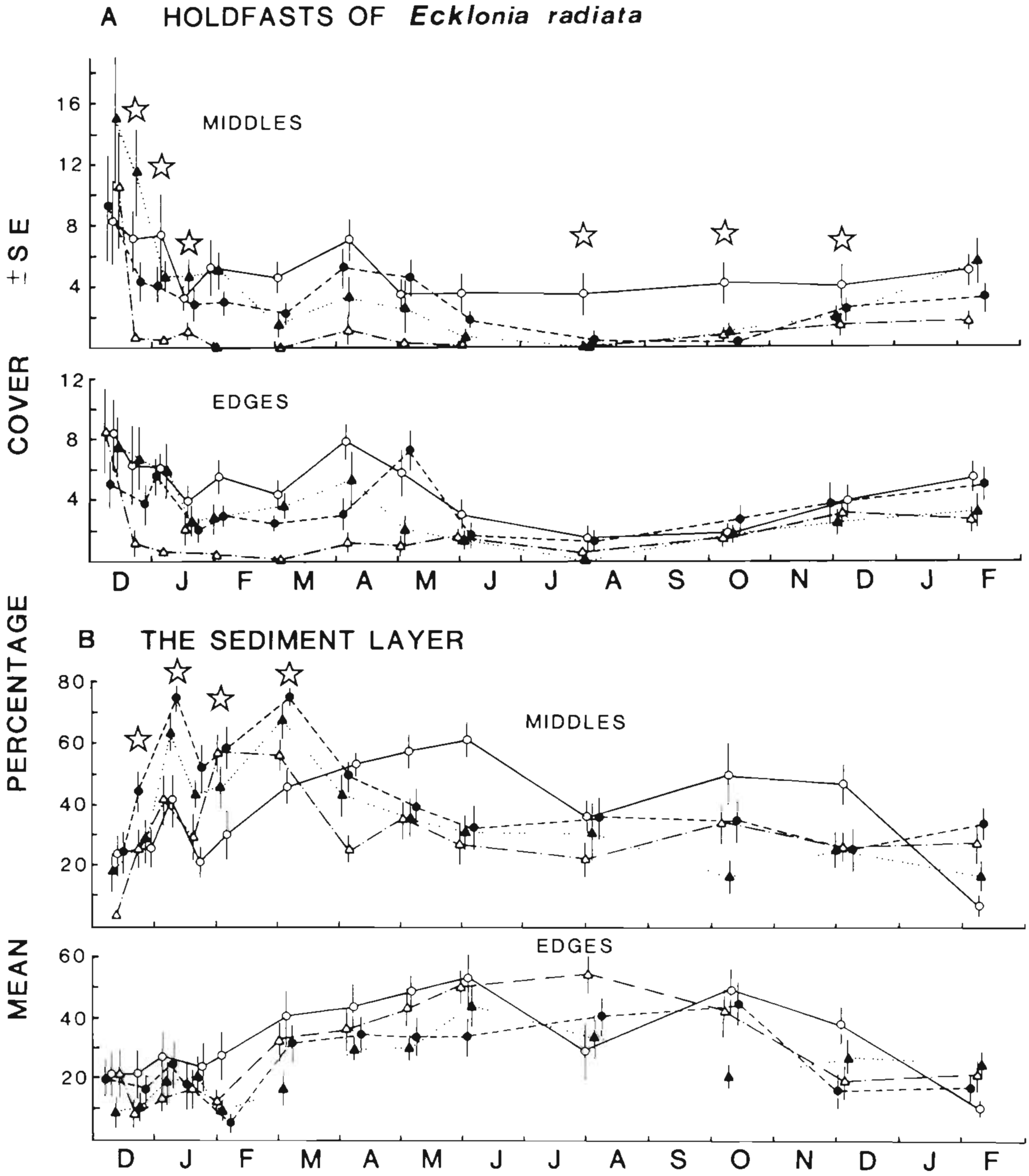

Fig. 2. Effects on the cover of (A) holdfasts of *Ecklonia radiata* and (B) the sediment layer due to differential damage to surrounding kelp plants *E. radiata*, in the middles and edges of experimental plots. For explanation of symbols, see legend to Fig. 1

stratum). Data for sessile microscopic species are presented as the relative cover (out of a maximum of 9 points). Microscopic animals were recorded as the total number of animals per quadrat. Organisms were identified as far as possible in the field, and samples were collected for further identification in the laboratory. A complete species list is presented in Table 2. Data for all species (recorded macroscopically and microscopically) were analysed by tests of homogeneity of variances, the relevant 2 or 3-factor analysis of variance and Student-Newman-Keuls multiple comparisons (significance level p = 0.05). Those sets of data that showed significant variation among experimental treatments are discussed below.

RESULTS

Expt 1. Effects of differential damage to kelp plants and effects of borders of clearings

The covers of the encrusting algae *Peyssonelia gunniana/Hildenbrandia prototypus* complex de-

Table 3. Summary of results from Expt 1. In this and subsequent tables, the time after manipulation at which an increase (+) or decrease (−) occurred is expressed in weeks. Maximum and minimum means for each species are given; all data are from macroscopic sampling (quadrat size: 900 cm^2) except those marked 'micro' (quadrat size: 25 mm^2)

Taxon	Range of means	Whole plants	Stipes & holdfasts	Holdfasts only	Totally cleared	Middles	Edges
Species that decreased after clearing							
• *Peyssonelia/Hildenbrandia*	(51–0 %)	ns	−8	−8	−8	−8	−20
Didemnum sp.	(22–0 %)	−12	−8	−8	−8	−8	−12
Myxilla sp.	(21–0 %)	−12	−4	−4	−4	−4	−12
Microscopic algae – initial occupiers of clearings							
Enteromorpha intestinalis (micro)	(0–33 %)	ns	+2 −12	+2 −12	+2 −12	+2 −12	ns
• *Giffordia mitchelliae* (micro)	(0–22 %)	ns	+6 −16	+6 −16	+6 −16	+6 −16	ns
Unicellular algae (micro)	(0–11 %)	ns	ns	ns	ns	ns	ns
Turf algae – occupied the substratum after filamentous algae							
• *Zonaria/Lobophora*	(0–60 %)	ns	+12 −44	+12 −44	+12 −44	+12 −44	+48
Colpomenia sinuosa	(0–16 %)	ns	+6 −8	+6 −8	+6 −8	+6 −8	ns
Sargassum spp.	(0–9 %)	ns	+12	+12	+12	+12	+40
Padina fraseri	(0–8 %)	ns	+12 −24	+12 −24	+12 −24	+12 −24	ns
Dictyota spp.	(0–6 %)	ns	+24 −48	+24 −48	+24 −48	+24 −48	ns
Haliptilon/Amphiroa	(0–2 %)	ns	+16 −32	+16 −32	+16 −32	+16 −32	+20
Recovery by kelp							
•• *Ecklonia radiata* holdfasts	(0–15 %)	ns	−8 +48	−8 +48	+48	−8 +48	−40
Abundances fluctuated – independent of clearing							
•• Sediment layer	(5–75 %)	+4 −56	+6 −56	+6 −56	+6 −56	+6 −56	+16
Fine silt (micro)	(0–75 %)	+12	+12 −48	+12 −48	+12 −48	+12	+16 −48
Ulva lactuca	(0–2 %)	+24 −32	+5 −32	+5 −32	+5 −32	+5 −32	ns

• Data set presented in Fig. 1. •• Data set presented in Fig. 2. ns: not significant ($p > 0.05$)

creased in all treatments and in the untouched controls (Fig. 1). An overall increase occurred 14 mo after clearing in all treatments. There was a significant trend after 2 mo towards less *Peyssonelia/Hildenbrandia* in the middles of clearings than on the edges. The microscopic alga *Giffordia mitchelliae* (Harvey) increased in abundance in the centres of all treatments with damaged kelp. This increase peaked after 2 mo, and the alga decreased again within 3 mo. The brown turf algae *Zonaria* spp./*Lobophora variegata* complex increased in cover in the centres of all clearings where kelp plants were damaged. Abundances decreased 11 mo after clearing. In uncleared control areas, no such change occurred. There was some increase in cover on the edges of clearings 9 mo after clearing.

The percentage cover of the substratum occupied by holdfasts of *Ecklonia radiata* was negligible for those areas where all the kelp was removed (Fig. 2). In the other damaged areas (i.e. minus laminae, and minus laminae and stipes) the cover of holdfasts decreased from their starting covers. This occurred within 2 mo after clearing and was more pronounced in the middles of areas than on the edges. The cover of *E. radiata* holdfasts gradually increased after 12 mo on the edges, and after 14 mo in the middles of clearings. The cover of the sediment layer (a mixture of fine silt, unicellular, filamentous algae, and micro-invertebrates) increased in the middles of all treatments after 4 wk. On the edges of experimental plots, the increase in cover of the sediment layer occurred after 3 mo. Cover of this layer began to decrease after 10 mo.

Table 3 summarizes results for all species that showed significant effects in Expt 1. The covers of encrusting algae, *Didemnum* sp. and *Myxilla* sp. all decreased in areas that had damaged kelp. Such decreases also occurred for *Didemnum* sp. and *Myxilla* sp. after longer periods in uncleared areas. While this was occurring, microscopic algae grew in those areas with damaged kelp canopies, but decreased in cover after a few weeks. This decrease of microalgae occurred after *Zonaria/Lobophora* complex, *Colpomenia sinuosa* (Roth) Derbes & Solier, *Sargassum* spp., *Padina fraseri* (Greville) and the red algae *Haliptilon* sp. and *Amphiroa* sp. increased in the areas with damaged kelp compared to uncleared controls. *Dictyota* spp. increased later in manipulated areas but decreased soon after. Then, some of the other turf species decreased in areas with damaged kelps, but the timing of these decreases was species-specific. *P. fraseri* dropped out of the community after 6 mo whilst *Zonaria/*

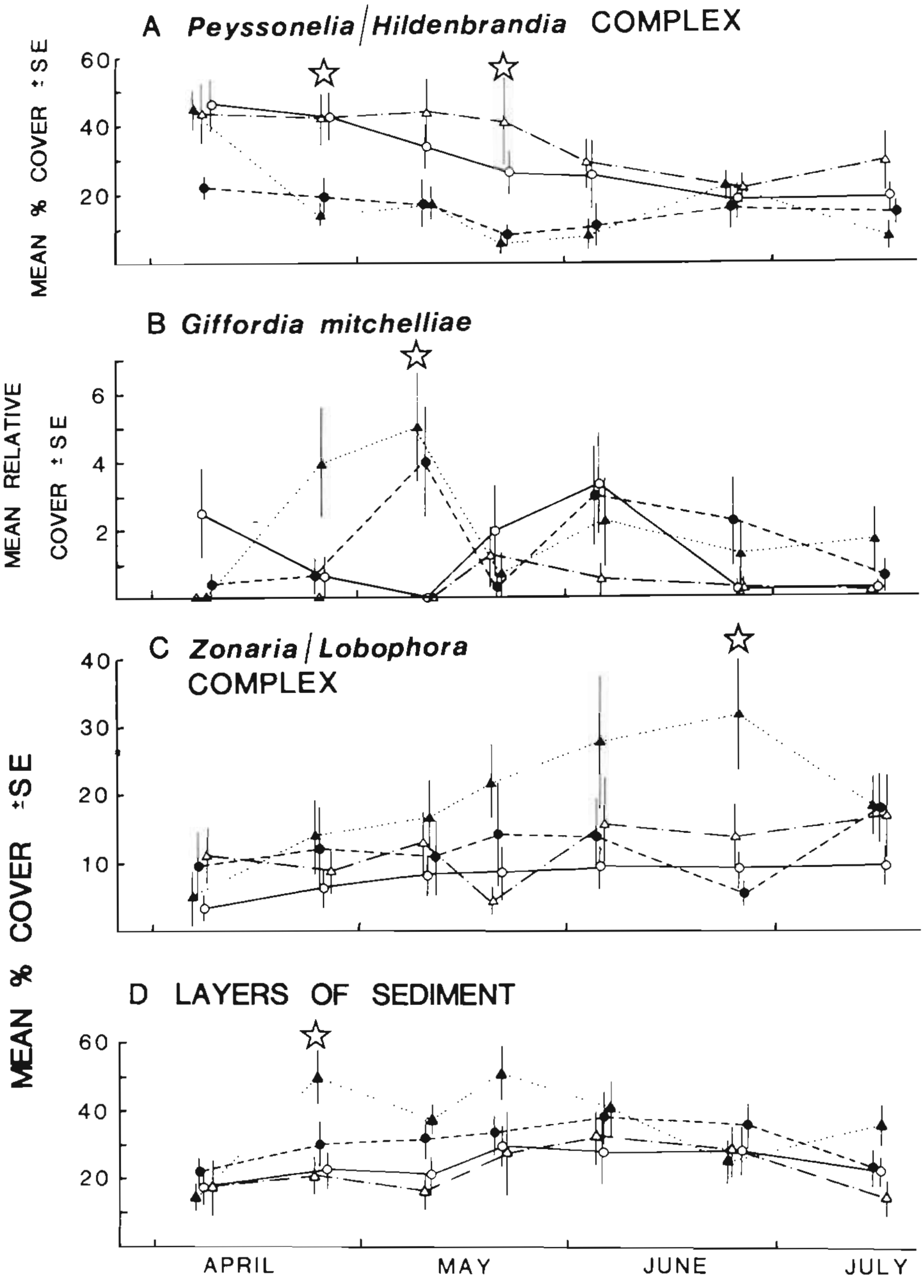

Fig. 3. Effects on the cover of (A) *Peyssonelia/Hildenbrandia* complex, (B) *Giffordia mitchelliae*, (C) *Zonaria/Lobophora* complex, and (D) sediment layer due to reducing density of kelp *Ecklonia radiata* canopy. Treatments were: (▲) fully cleared of kelp; (△) half cleared of kelp; (●) quarter cleared of kelp; and (○) natural, uncleared areas of kelp. (n = 9)

Lobophora complex, *Haliptilon* sp. and *Amphiroa* sp. persisted for longer periods. *Sargassum* spp. was still present after 14 mo. The decrease in covers of *Zonaria/Lobophora* complex coincided with the arrival of *E. radiata* into areas after 12 mo (shown by the gradual increase in the cover of holdfasts of *E. radiata* [Table 3], first on edges of clearings and then in the centres). The covers of the sediment layer, fine silt (sampled microscopically) and the green alga, *Ulva lactuca* (Linnaeus), fluctuated in all experimental treatments. These changes of silt and *U. lactuca* were independent of experimental manipulations. The above changes (Table 3) took place in all 3 damaged treatments showing that the partial denudation of kelp plants had similar effects on understorey species as did their total removal.

The changes due to kelp damage occurred mainly in the middle of experimental plots where influences of the surrounding kelp canopy were least (Table 3). On the edges of plots, the abundances of some species (encrusting algae, *Didemnum* sp., *Myxilla* sp., *Sargassum* spp., *Haliptilon* sp. and *Amphiroa* sp.) showed similar, though delayed responses to those found in the middles. Other species on edges showed no effects due to damage of the kelp. The percentage cover of sediment on edges of manipulated areas increased more slowly than in the middles of clearings – probably a result of differential entrapment of sediment due to different flora and microtopographies. In summary, the assemblage of understorey species on edges of clearings showed a response intermediate between those of the middles of clearings and those of uncleared areas, both in terms of species composition and the timing of the presence of species.

Expt 2. Effects of removal of different densities of kelp plants

Peyssonelia/Hildenbrandia complex decreased in cover in uncleared areas, in areas cleared of all kelp and in areas with half the kelp removed (Fig. 3). Areas that had one quarter of the kelp plants removed began with little cover of *Peyssonelia/Hildenbrandia* complex, and cover remained low. Within 2 wk of clearing, cover in totally cleared treatments had dropped from around 45 to 15 %. The cover of these encrusting algae in uncleared and half cleared treatments declined gradually after 1 mo. *Giffordia mitchelliae* increased in cover in totally cleared areas after 2 wk. A similar increase occurred for the quarter cleared treatment after 4 wk. *Zonaria/Lobophora* complex showed no changes in cover in any treatments except the fully cleared areas. In these areas, the cover of *Zonaria/Lobophora* complex gradually increased over 2½ mo before decreasing again to low levels. The cover of the sediment layer increased slightly in those treatments that were totally cleared of kelp. This only occurred during the first 6 wk after clearing.

Table 4 summarizes those effects on the community due to reducing the kelp canopy to various densities. Some species (*Zonaria/Lobophora, Ulva lactuca, Dictyota* spp.) and sediment increased in areas that were fully cleared of kelp but not in half, quarter, or uncleared areas. The covers of *Rhodymenia* sp., *Sargassum* spp. and juveniles of *Ecklonia radiata* increased in all treatments, including uncleared controls, suggesting no effects due to thinning the canopy. Effects of canopy density on the establishment of these species may occur, however, at other times of the year when these species recruit in greater densities. The cover of *Didemnum* sp. increased in uncleared and quarter cleared treatments, showing that greater reduction of the kelp canopy (up to half the plants removed) affects its growth. Unicellular and filamentous algae showed increases in the quarter and fully cleared treatments, but not in the half or uncleared areas – implying no consistent effects due to thinning the canopy. Fine silt settled in all areas that had some or all kelp removed, indicating a general increase of silt in manipulated areas compared to uncleared controls. In summary, partial reduction in the kelp canopy causes increases in abundance for some species, but for others only total clearing of the canopy will cause changes in abundances.

Expt 3. Effects on understorey species of provision of bare space

The cover of unicellular algae increased initially in all bare areas and remained abundant in areas at Site 3, but decreased at Sites 1 and 2 (Fig. 4). The cover of *Giffordia mitchelliae* on bare areas increased after

Table 4. Summary of results from Expt 2: effects of thinning the kelp canopy. See Table 3 for explanation

Taxon	Range	Uncleared	Quarter cleared	Half cleared	Totally cleared
Species showing effects of thinning the canopy					
•*Peyssonelia/Hildenbrandia*	(5–50 %)	−6	−8	−10	−2
•*Zonaria/Lobophora*	(0–31 %)	ns	ns	ns	+10
Didemnum sp.	(0–10 %)	+10	+10	ns	ns
Dictyota spp.	(0–7 %)	ns	ns	ns	+6 −10
Ulva lactuca	(0–5 %)	ns	ns	ns	+4 −8 +10
•Sediment layer	(17–45 %)	ns	ns	ns	+2 −8
Fine silt (micro)	(0–66 %)	ns	+8 −10	+8 −10	+8 −10
Fluctuating abundances independent of thinning canopy					
•*Giffordia mitchelliae* (micro)	(0–56 %)	ns	+4 −6	ns	+4 −6
Unicellular algae (micro)	(0–3 %)	ns	+4 −6	ns	+2 −6
Rhodymenia sp.	(0–3 %)	+14	+14	+14	+14
Sargassum spp.	(0–3 %)	+14	+14	+14	+14
Juvenile *Ecklonia*	(0–3 plants)	+14	+14	+14	+14

• Data set presented in Fig. 3. ns: not significant ($p > 0.05$)

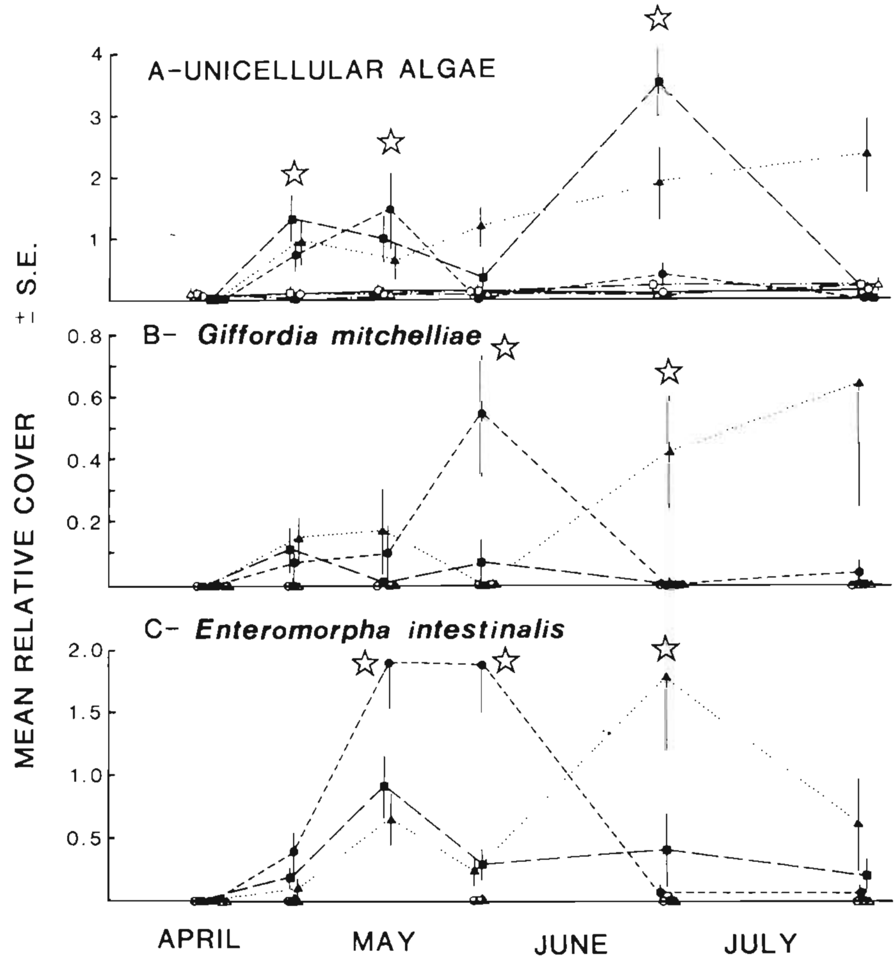

Fig. 4. Effects on the cover of (A) unicellular algae, (B) *Giffordia mitchelliae*, and (C) *Enteromorpha intestinalis* (sampled with the underwater microscope) after removing all species from the substratum and exposing bare rock. Treatments were: areas of bare rock at (■) Site 1, (●) Site 2, (▲) Site 3; and uncleared areas of substratum covered by encrusting algae and sponges at (□) Site 1, (○) Site 2 and (△) Site 3. (n = 28)

Table 5. Summary of results from Expt 3: colonization of areas of bare substrata. See Table 3 for explanation. (N.B. All data are from microscopic sampling (quadrat size: 25 mm^2)

Taxon	Range	Site 1	Site 2	Site 3
Ulva lactuca	(0–61 %)	+10	ns	ns
•Unicellular algae	(0–38 %)	+4 −6	+2 −6 +10 −14	+10
•*Enteromorphia intestinalis*	(0–22 %)	+4 −10	+4 −6	+4 +10 −14
•*Giffordia mitchelliae*	(0–7 %)	+6 −10	ns	+10
Ceramium sp.	(0–16 %)	+4	+4	+4 −6 +10 −14
Rhodymenia sp.	(0–15 %)	+10	ns	ns
Blue-green algae	(0–7 %)	+2 −4	+2 −4	+2 −4
Invertebrates	(0–1.1 animals)	+4 −6	+4 −6	+4 −6
Neogoniolithon sp.	(0–66 %)	+10	+10 +14	+10 +14
Fine silt	(0–53 %)	+6	+6	+6
Bare substrata	(100–0 %)	–	–	–

• Data set presented in Fig. 4. ns: not significant ($p > 0.05$)

6 wk at Site 2 before declining after 8 wk. This species also increased after 10 wk at Site 3. No such increase occurred at Site 2. The cover of *Enteromorpha intestinalis* (Linnaeus) Link increased in all bare areas and remained great in areas at Site 2 before decreasing. Bare areas at Site 3 increased in cover of *E. intestinalis* after a longer period.

Table 5 summarizes the results for species in Expt 3. After an initial colonization and subsequent decrease of blue-green algae in all bare areas, species such as *Enteromorpha intestinalis*, *Ceramium* sp., *Neogoniolithon* sp. and microscopic invertebrates increased in abundances; the latter may have been attracted to the filamentous algae as a source of food

(Kennelly 1983, Kennelly 1987). Silt also settled equally in all areas. Other species only increased at certain sites (*Ulva lactuca, Giffordia mitchelliae, Rhodymenia* sp.). At Site 1, unicellular algae, *E. intestinalis* and *G. mitchelliae* all increased and then decreased as other species occupied the substratum (*Ceramium* sp., *Rhodymenia* sp. and finally *Neogoniolithon* sp. and *U. lactuca*). At Site 2, *Ceramium* sp. and *Neogoniolithon* sp. eventually occupied the substratum after decreases in the covers of the early colonists (unicellular algae and *E. intestinalis*). At Site 3, unicellular algae, *G. mitchelliae* and *Neogoniolithon* sp. occurred later, after the earlier establishment by *E. intestinalis* and *Ceramium* sp.

DISCUSSION

The results from Expt 1 showed that physical disturbances that remove kelp fronds, or fronds and stipes, have the same effects on kelp populations and understorey species as the complete removal of plants. Observations revealed that damage to kelp plants which results in tissue loss above the primary meristem (by storms and/or feeding by odacid fish) leads to the recovery of the fronds and so negligible effects on the canopy and understorey species.

The effects on understorey species of living on the edges of clearings were found to be intermediate between those occurring in the middles of clearings and those under the canopy. This was evidenced by both quantitative differences in abundances and the delayed responses of species to physical perturbation. Such responses are common effects of borders (Dayton & Oliver 1980).

In partial clearances (Expt 2) most species behaved as they did in totally cleared treatments, whilst others required at least 50 % removal of the overlying canopy to affect abundances. Thus, for most species, results of partial clearances are consistent with results of previous studies of physical disturbances in kelp forests where only uncleared and fully cleared plots were examined (Chapman 1984, Reed & Foster 1984, Santelices & Ojeda 1984). For other species, physical disturbances that only partially remove kelp canopies had very different effects on abundances. Partial clearances occur quite regularly in kelp communities, whilst total clearances require quite large perturbations, such as heavy storms and El Niño events (Dayton et al. 1984, Gerard 1984). This stresses the need for experiments concerning physical disturbances in kelp forests to include different degrees of perturbation.

The results from Expt 3 illustrated influences on the development of understorey communities following the removal of kelp holdfasts and the availability of new primary substratum. These data showed that filamentous species such as *Ceramium* sp., *Giffordia mitchelliae* and unicellular algae dominated the substratum early in some areas, and later in other areas. This indicated that, following the dislodgement of holdfasts, the establishment of species on small areas of bare substrata depended upon the recruitment of each species to these areas. This could be because different locations, with different 'spore rains' had different assemblages developing. Alternatively, post-settlement survival was different in different areas. After about 12 mo, however, those species that best tolerate low light levels under the canopy (encrusting algae, sponges and ascidians) eventually dominated these areas.

This research reveals that simple canopy-removal experiments do not consider the many effects that species may experience when physical disturbances occur in kelp communities. Such factors as the severity of disturbance, the location of propagules of individual species, and the presence of clean primary substrata all act to determine community structure following perturbations. These factors act in concert with factors concerning the timing of disturbances and temporal fluctuations in abundances of species as addressed elsewhere (Kennelly 1987). Future work along these lines should take these complicating factors into account. Further, because the responses of individual species to these factors differ, future work should include the comprehensive sampling of the species assemblage.

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