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Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs

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Abstract

Changes in assemblages of plants, macroinvertebrates and fishes on three eastern Tasmanian reefs were monitored over 12 months in replicated control blocks and adjacent 10×12-m blocks cleared of fucoid, laminarian and dictyotalean algae. Removal of canopy-forming plants produced less change to biotic assemblages than reported in studies elsewhere, with the magnitude of change for fish and invertebrate taxa lower than variation between sites and comparable to variation between months.

The introduced annual kelp *Undaria pinnatifida* exhibited the only pronounced response to canopy removal amongst algal taxa, with a fivefold increase in cleared blocks compared to control blocks. Marine reserves are suggested to assist reef communities resist invasion by *U. pinnatifida*, through an indirect mechanism involving increased predation pressure on sea urchins and reduced formation of urchin barrens that are amenable to *U. pinnatifida* propagation.

Large invertebrates were more associated with turfing algae or the reef substratum than the macroalgal canopy. The herbivorous sea urchin *Heliocidaris erythrogramma* and abalone *Haliotis ruber* showed the strongest response to clearing amongst common macroinvertebrate species, with a halving of population numbers. Observed densities of the common monacanthid fish *Acanthaluteres vittiger* also declined by about 50%. The relatively high level of resistance shown by eastern

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Tasmanian reef biota to patch disturbance was attributed largely to high diversity and biomass of turfing macroalgae damping effects of canopy clearance.

Keywords: Algal canopy; Experimental clearance; Invertebrate; Marine protected area; Sublittoral; *Turbo undulatus*; *Undaria pinnatifida*; Urchin barrens

1. Introduction

Sunlit temperate reefs worldwide are typically either dominated by dense beds of laminarian or fucoid algae, or comprise open areas of substrata with a predominant cover of coralline algae (Tegner and Dayton, 2000). Open areas can be carpeted by articulated corallines and other turfing algae (Fowler-Walker and Connell, 2002), or, more often, consist of 'barren grounds' (Andrew and Underwood, 1989)—bare coralline-algal-encrusted rock that persists as a result of overgrazing of macrophytes by sea urchins and other herbivorous invertebrates. Macroalgal-beds and open barren grounds can vary over short spatial and temporal scales, and in many areas represent alternate states (Ebling et al., 1985; Harrold and Reed, 1985; Chapman and Johnson, 1990; Tegner and Dayton, 1991; Shears and Babcock, 2003).

Numerous observational and experimental studies have been undertaken in barren grounds, with general agreement amongst investigators that the biota inhabiting such areas is quite different from that present in algal-dominated areas (Schiel and Foster, 1986; Tegner and Dayton, 2000). For example, elimination of the kelp *Ecklonia radiata* by the echinoid *Centrostephanus rodgersii* in New South Wales causes increased encrusting coralline algal cover and grazing limpet densities (Fletcher, 1987), and is associated with declines in abalone populations (Andrew et al., 1998). In New Zealand, macroalgal-dominated reefs and barren grounds differ substantially in overall primary and secondary productivity (Babcock et al., 1999).

Barren grounds have probably expanded globally during the past half century following widespread over-harvesting of sea urchin predators, as indicated by increasing urchin population density and decreasing kelp coverage in the northwestern Pacific, northwestern Atlantic and Mediterranean since the 1950s (Pinnegar et al., 2000; Tegner and Dayton, 2000). In eastern Tasmania, urchin barrens have become much more widespread during the past two decades, primarily as a consequence of increasing abundance and the southward range extension of *C. rodgersii*, a species not recorded in the region prior to the late 1970s (Edgar, 1997). Given the potential magnitude of change associated with the local arrival of this urchin, and concern expressed by local fishers about likely fisheries impacts (C.R. Johnson, personal communication), we here describe experimental manipulations aimed at assessing the importance of canopy algae to common species on Tasmanian reefs.

Our experiments were also initiated in part because of a lack of information on ecosystem consequences of the regional decline in giant kelp (*Macrocystis pyrifera*) beds since the 1980s (Crawford et al., 2000), and because of changes in algal composition observed during long-term monitoring of Tasmanian marine protected areas (MPAs; Edgar and Barrett, 1999). The sparse information available on interactions between kelp, invertebrates and fishes at the scale of habitat patches on reefs was considered inadequate for confident interpretation of community changes in MPAs following prohibition of fishing, particularly cascades involving urchin populations, macroalgal cover and other taxa (Babcock et al., 1999; Shears and Babcock, 2003).

Numerous studies have been published on effects of algal canopy clearance; however, very few, primarily manipulations of *M. pyrifera*, have been conducted for large clearance areas of 100–10,000 m^2, the grain size typical of the scale of habitat patchiness on reefs.

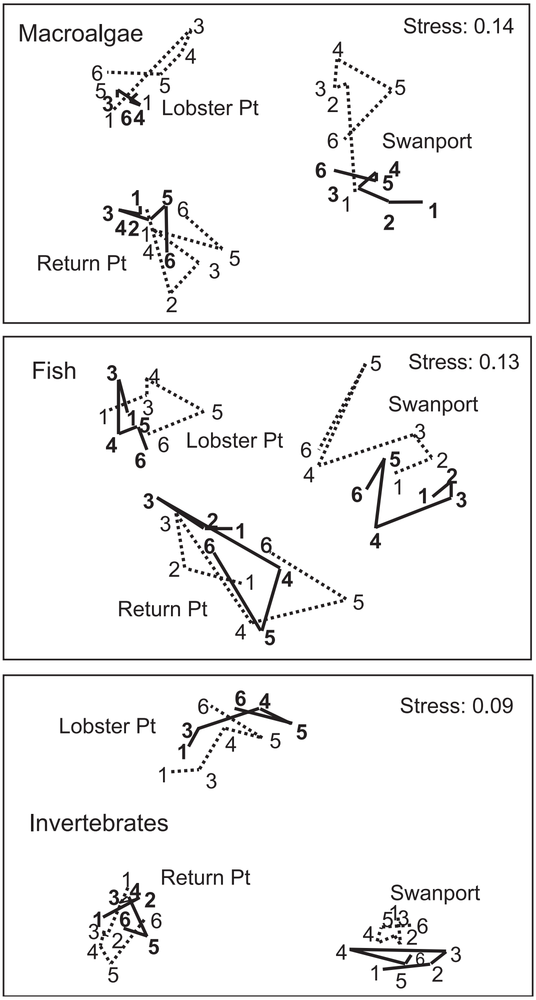

Fig. 1. MDS plots showing changes in macroalgal, fish and macroinvertebrate assemblages following canopy removal experiment. Changes over time in blocks cleared of macroalgae are shown with dashed arrows and in control blocks with solid arrows. Sampling occasions are 1: before; 2: 1 week post-disturbance; 3: 1 month post-disturbance; 4: 3 months post-disturbance; 5: 6 months post-disturbance; 6: 1 year post-disturbance.

Table 1
Mean-square values and degrees of freedom (*df*) generated by repeated-measure ANOVAs using data on species richness and percentage cover of macroalgal taxa with factors site, algal clearance and sampling occasion

Treatment	Mixed model	*df*	Algal species richness	Algal cover	Kelp cover	*Caulerpa* spp.	Foliose red algae	Branched coralline algae	*Undaria pinnatifida*
Site (S)	S/E1	2	155.0*	60800**	75987**	1592	506	36.4*	838*
Clearance (C)	C/S*C	1	731.1$^{\#\#\#}$	372900*	374857**	344	534	9.1	1293$^{\#}$
S*C	S*C/E1	2	63.9	4900	21	1878	560	8.5	541
Error1 (E1)		6	16.2	3000	4097	613	160	6.0	110
Occasion (O)	O/O*S	3	3.6	8000$^{\#}$	5053	1233$^{\#\#\#}$	830$^{\#}$	48.5	1401$^{\#\#\#}$
O*S	O*S/E2	6	14.4	4000	3093	290*	849**	17.0	2624***
O*C	O*C/O*S*C	3	43.9$^{\#\#}$	10500$^{\#}$	7826$^{\#}$	258	234	4.2	698$^{\#\#}$
O*S*C	O*S*C/E2	6	22.1	3500	3240	588**	233	1.1	1299***
Error2 (E2)		18	8.7	2100	1966	109	196	16.3	125

Significance was initially assessed using *F*-tests based on a mixed model with site considered a random factor: ***, $p<0.001$; **, $0.001<p<0.01$, *, $0.01<p<0.05$. For nonsignificant results, a model with site considered fixed was also applied: $^{\#\#\#}$, $p<0.001$; $^{\#\#}$, $0.001<p<0.01$; $^{\#}$, $0.01<p<0.05$.

The majority of published studies involving experimental clearance of algae has been conducted at a grain size of 1–20 m^2 (e.g., (Kennelly, 1987; Kennelly and Underwood, 1993; Machado et al., 1996), although some information on effects of algal disappearance is also available at broad geographic scales as a consequence of human overexploitation of kelp (Moreno, 2001). Large clearance areas are necessary if effects of algal loss on reef fishes are to be investigated because reef fish typically possess home ranges >2000 m^2 (Barrett, 1995). Large cleared areas may also be important for studies of invertebrates such as sea urchins that move several metres per night, and for kelps with restricted spore shadows that do not penetrate more than a few metres into open habitat (Paine, 1979; Kendrick and Walker, 1991).

Table 2
Mean-square values and degrees of freedom (*df*) generated by repeated-measure ANOVAs using data on species richness and log(x+1) abundance of fish taxa with factors site, algal clearance and sampling occasion

Treatment	*df*	Fish species richness	*Acanthaluteres vittiger*	Neoodax balteatus	*Notolabrus fucicola*	*Notolabrus tetricus*	*Pictilabrus laticlavius*	*Trachinops caudimaculatus*
Site (S)	2	1.1	8.0	0.52	35.0**	6.10	0.68*	3.2
Clearance (C)	1	41.1	32.7*	1.16	0.2	14.13*	5.93$^{\#\#\#}$	5.8
S*C	2	3.3	1.7	0.80	2.2	0.57	1.93**	7.8
Error 1 (E1)	6	60.4	2.6	2.37	2.5	2.23	0.10	23.6
Occasion (O)	3	207.6$^{\#\#\#}$	25.5$^{\#\#\#}$	4.77$^{\#\#\#}$	2.3	9.30$^{\#\#\#}$	9.41$^{\#\#\#}$	17.5$^{\#\#}$
O*S	6	144.7***	13.7***	1.41**	3.0	3.06**	3.84***	7.8*
O*C	3	3.8	2.4	0.65	2.8	1.58	0.43	3.1
O*S*C	6	2.7	2.0	0.2	2.1	0.33	0.21	1.5
Error 2 (E2)	18	7.9	2.3	0.32	1.2	0.64	0.34	2.3

Significance was initially assessed using *F*-tests based on a mixed model with site considered a random factor: ***, $p<0.001$; **, $0.001<p<0.01$, *, $0.01<p<0.05$. For nonsignificant results, a model with site considered fixed was also applied: $^{\#\#\#}$, $p<0.001$; $^{\#\#}$, $0.001<p<0.01$.

A second aspect of scaling that has restricted general applicability of conclusions of algal clearance studies is a lack of site replication. Whereas investigators are invariably concerned with replication at the within-site (1–1000 m) scale, few describe patterns over scales >1 km, and therefore only narrow inferences associated with particular sites can be made. This problem was recognised inter alia by Melville and Connell (2001) when discussing inconsistent responses in encrusting coralline algal cover generated in different studies after removal of the kelp *E. radiata*. Encrusting coralline algae are apparently affected nonlinearly by kelp clearance at different kelp densities, responding in opposite directions in experimental clearances at sites with low and high initial cover of kelp. Meta-analysis of results from sites studied individually can also overemphasise environmental variability at the expense of the ability to detect widespread pattern (Fowler-Walker and Connell, 2002). Our study provides information relating to a clearance size of 600 m^2 and 50 km span of sites.

2. Methods

2.1. Sites studied

Experiments were undertaken at three rocky reef sites in eastern Tasmania that were surveyed during the week prior to algal canopy clearance and within 4 to 5 day 'sampling occasions' at intervals of 1 week, 1, 3, 6 months and 1 year after clearance at each site. Surveys commenced on 21 Feb 2000 at Return Point (42.633°S 148.025°E), 3 Oct 2000 at Little Swanport (42.276°S 148.015°E) and 6 Feb 2001 at Lobster Point (42.964°S 147.667°E). Because of poor weather, sampling at Lobster Point was omitted on the 1-week sampling occasion.

Table 3
Mean-square values and degrees of freedom (*df*) generated by repeated-measure ANOVAs using data on species richness and log(x+1) abundance of macro-invertebrate and cryptic fish taxa with factors site, algal clearance and sampling occasion

Treatment	*df*	Invertebrate species richness	Fish species richness	*Cenolia trichoptera*	*Haliotis ruber*	*Heliocidaris erythrogramma*	*Tosia australis*	*Turbo undulatus*	*Scorpaena ergastulorum*
Site (S)	2	120.8*	15.05	9.77	17.34**	1.16	5.53	95.0*	4.10
Clearance (C)	1	54.1	0.18	1.48	$8.39^{\#}$	$9.99^{\#}$	2.68	40.1	0.03
S*C	2	9.0	2.28	1.23	7.07*	4.85	3.19	12.2	1.18
Error 1 (E1)	6	15.8	3.88	3.42	1.09	1.19	1.20	10.2	1.36
Occasion (O)	3	$14.1^{\#}$	$8.57^{\#\#\#}$	0.28	1.03	$2.54^{\#}$	$2.18^{\#}$	1.5	$1.74^{\#\#}$
O*S	6	10.5*	4.00**	0.85*	1.05	1.99	3.22**	0.5	1.16**
O*C	3	1.9	0.31	0.38	0.28	1.41	0.37	0.5	0.22
O*S*C	6	3.1	1.06	0.11	0.37	0.94	0.23	0.6	0.24
Error 2 (E2)	18	3.0	0.94	0.24	1.00	0.80	0.55	1.7	0.22

Significance was initially assessed using F-tests based on a mixed model with site considered a random factor: ***, $p<0.001$; **, $0.001<p<0.01$, *, $0.01<p<0.05$. For nonsignificant results, a model with site considered fixed was also applied: $^{\#\#\#}$, $p<0.001$; $^{\#\#}$, $0.001<p<0.01$; $^{\#}$, $0.01<p<0.05$.

On each sampling occasion, a single 200-m transect line was laid subtidally parallel with the shore in 3–6-m water depth. The transect line was relocated within 1 m of initial position on each sampling occasion by reference to permanent markers on the seabed. Reef at all sites was bounded at its deeper edge in 5–7-m depth by sand and extended in a 30–70-m-wide strip along the coast. The sandstone reef at Lobster Point was heavily dissected with numerous rocks and crevices, whereas the low dolerite reefs at Return Point and Little Swanport were less structurally heterogeneous but possessed occasional boulders, shelves and crevices. Habitats at all sites were dominated by a variety of fucoid and laminarian algal species. *E. radiata* and *Sargassum verruculosum* were predominant at Lobster Point, *Cystophora subfarcinata*, *Cystophora moniliformis*, *Caulocystis cephalornithos*, *Sargassum decipiens* and *S. verruculosum* at Return Point, and *Phyllospora comosa* at Little Swanport. Taxonomic authorities for all plant and animal species mentioned are listed by Edgar (1997).

2.2. Algal clearance experiments

The relationship between macroalgal cover and densities of reef species was assessed by divers pulling out by hand all large laminarian, fucoid and dicyotalean algae from two 50-m-long, 12-m-wide blocks at each site. The cleared blocks were centred on the censused transect line, and separated by 50-m distance; hence, two 50-m cleared and

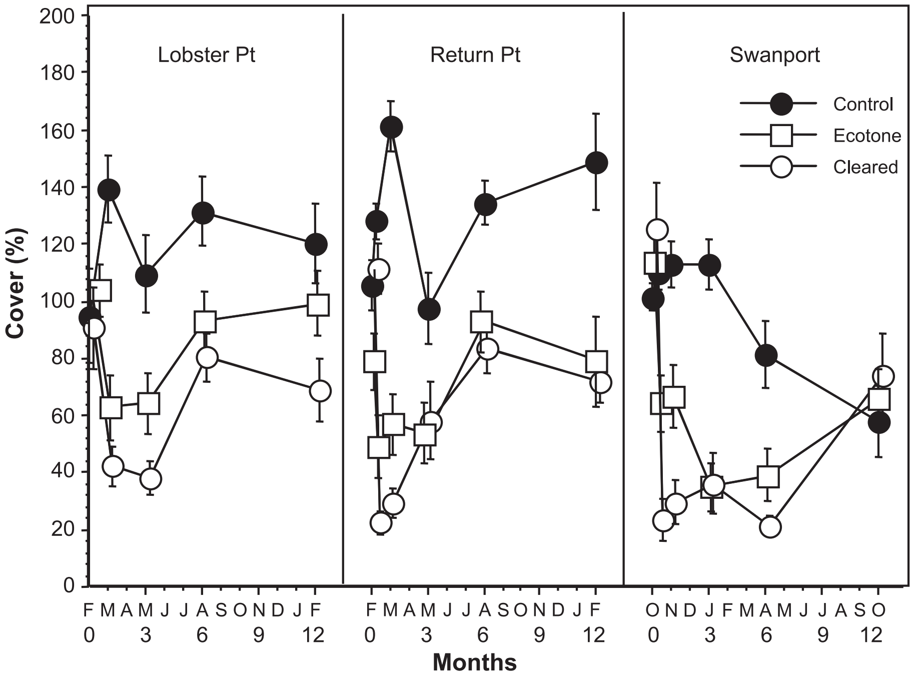

Fig. 2. Mean changes in plant cover (±S.E.) during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

control blocks alternated along the transect. The experimental design was thus comparable to an agricultural experiment with contiguous alternating manipulated and control blocks (Snedecor and Cochran, 1967).

2.3. Survey techniques

Quantitative surveys of (i) large fishes, (ii) large macroinvertebrates and cryptic fishes, and (iii) plants were undertaken using visual census protocols described previously for reef monitoring studies of Tasmanian MPAs (Edgar and Barrett, 1997, 1999; Edgar et al., 1997). Visual censuses can involve substantial bias; nevertheless, these techniques were considered appropriate here because biases are largely systematic and should not greatly affect relative comparisons (Edgar et al., 2004). All surveys at a site commenced at the centre of the transect line and comprised a manipulated followed by a control block in one direction, then a control block followed by a manipulated block in the other.

For estimates of large fishes, a diver swam beside the transect line at a distance of 2.5 m, recording on a waterproof notepad the abundance and size structure of fishes in a 5-m-wide swathe out from the line. The diver swam slowly, estimating the number of the different fish species sighted within each 10-m length of transect. The survey process was then repeated by the diver returning along the other side of the transect line, with data from

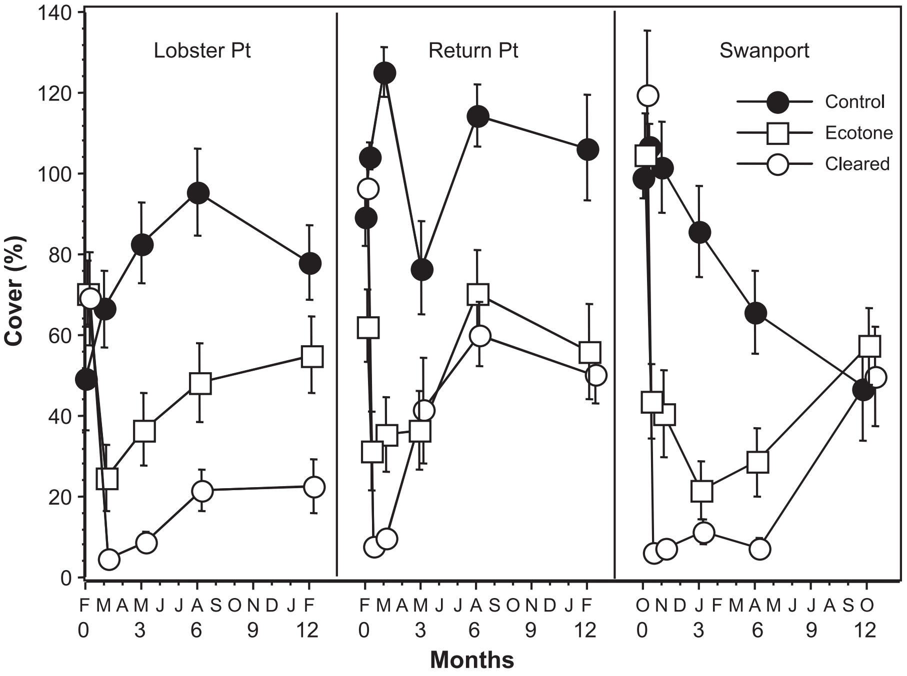

Fig. 3. Mean changes in cover (±S.E.) of 'kelp' (fucoid and laminarian algae) during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

two adjoining sides of the transect added together. Twenty 10×10-m blocks were thus censused, with data from 10×50-m blocks usually aggregated, corresponding to four treatment blocks. Five replicate surveys were generally conducted on each sampling occasion.

Large macro-invertebrates (echinoderms other than ophiuroids, large molluscs, large crustaceans) and cryptic fishes were counted along transect lines by recording animals in the same 10-m transect intervals as used for the fish survey, but within 1 m of one side of the line. Three replicate surveys were generally undertaken on each sampling occasion.

Plant cover was quantified by placing a 0.25-m^2 quadrat at 10-m intervals along alternating sides of the transect line and estimating the percentage area of reef substrata covered by different macroalgal species. Percentage cover was assessed by counting the number of times each species occurred directly under 50 positions on the quadrat at which perpendicularly placed wires crossed each other. Canopy-forming algae were moved aside for determinations of turfing algal cover, hence total percentage cover of plants exceeded 100% when a dense algal canopy overlaid a layer of turfing plants. Quadrats were located at the midpoint of the 10-m-long blocks used for fish and macro-invertebrate counts. Two replicate surveys, occasionally more, were undertaken on each sampling occasion.

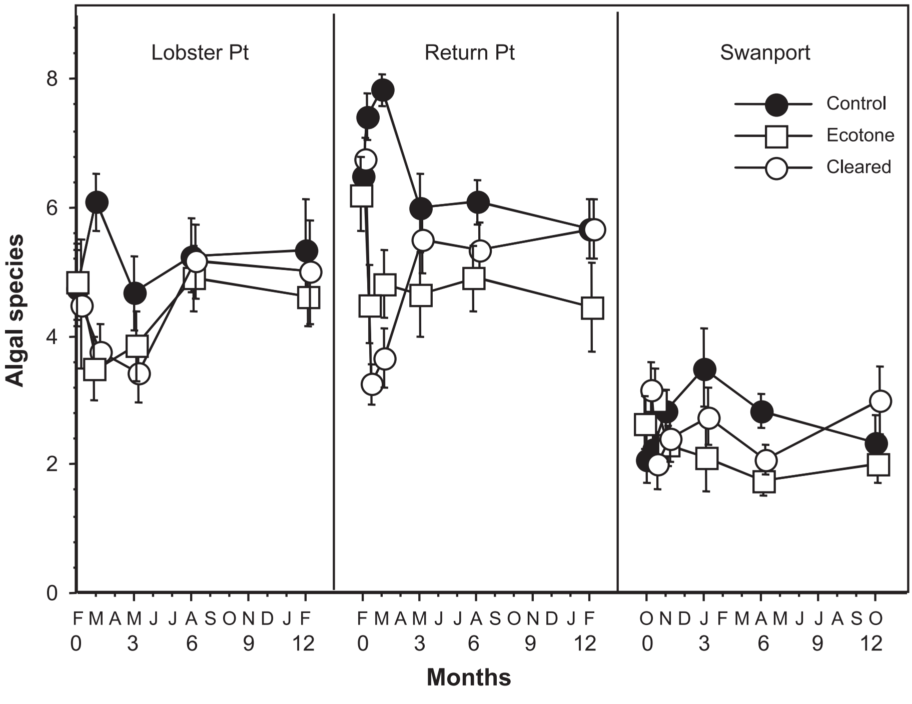

Fig. 4. Mean changes in total number of algal species per quadrat during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

2.4. Data interpretation

Relative changes over time in the plant and animal communities in cleared and control areas were initially examined graphically using nonmetric multidimensional scaling (MDS). The data matrices used for MDS were ln(x+1) transformed for faunal abundance data but not algal percent cover data, and then converted to a symmetric matrix of biotic similarity between pairs of sites using the Bray–Curtis similarity index (Clarke, 1993). MDS plots reduce multidimensional patterns of biotic similarity to the best two-dimensional representation, with a stress statistic indicating the extent to which multidimensional variation is encompassed within the two dimensions. Clarke (1993) suggested that an MDS display is poor if the stress statistic exceeds 0.2.

Effects of algal clearance on abundance of individual taxa and assemblage species richness were examined using repeated-measures analysis of variance (ANOVA). Taxa analysed using ANOVA were the most abundant and widely distributed species plus taxonomic groups considered potentially important. Data for sand and encrusting coralline algal cover were not analysed because the quadrat method proved unreliable for accurate determination of these variates. Divers experienced difficulty consistently quantifying live encrusting coralline algae from within a complex mosaic of living, bleached and dead plants interspersed amongst turfing algae, while cover of sand was

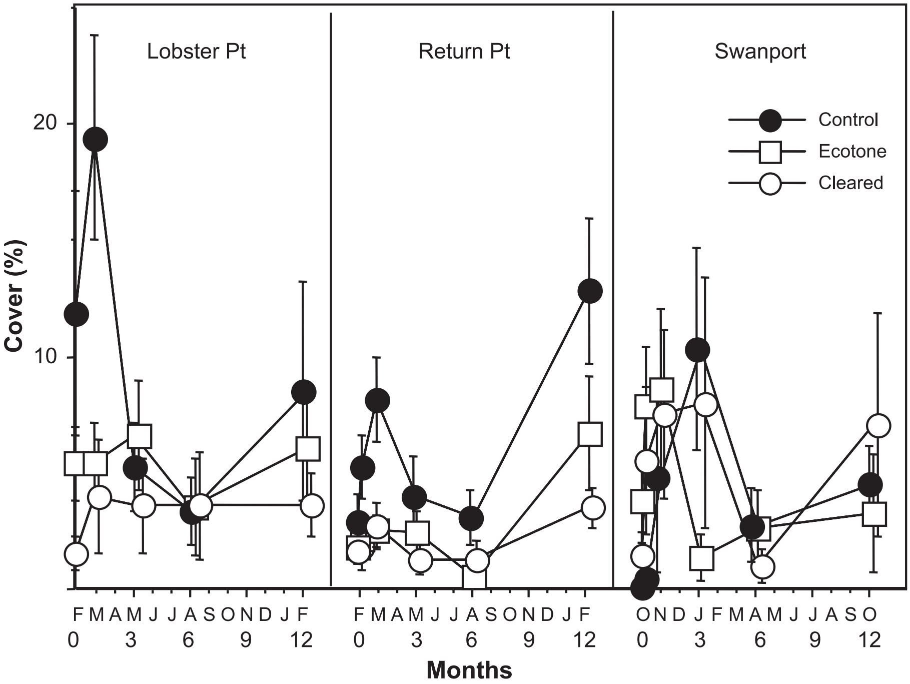

Fig. 5. Mean changes in total cover (±S.E.) of eight species of *Caulerpa* during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

negligible amongst holdfasts and rhizoids of plants, and in cracks and depressions between boulders.

For each of the three sites, data for each sampling occasion were amalgamated for ANOVA as a mean value within each of the four sampling blocks (two cleared and two control). Given that the first sampling occasion provided baseline data against which subsequent post-clearance changes were compared, the dependent variable investigated was mean abundance or species richness within a block less the mean baseline value for that block. Abundance data were ln(x+1) transformed to reduce heteroscedasticity, and because multiplicative changes were considered more important than additive changes.

The ANOVA model included two orthogonal factors, ‘clearing’ (i.e., cleared and control) and ‘site’ (Lobster Point, Return Point, Little Swanport), and the repeated measure ‘sampling occasion’ (n=4; 1-week sampling occasion omitted to maintain a balanced design). A repeated measures model was necessary because the same blocks were surveyed and used as replicates on each sampling occasion.

A general model was initially examined with ‘site’ considered a random factor, and ‘clearing’ fixed. The power of some F-tests using this model was low because only three sites were investigated. Consequently, treatments found nonsignificant were reexamined with ‘site’ considered a fixed factor. A significant outcome for the fixed factor analysis but not the mixed model implies a significant treatment effect

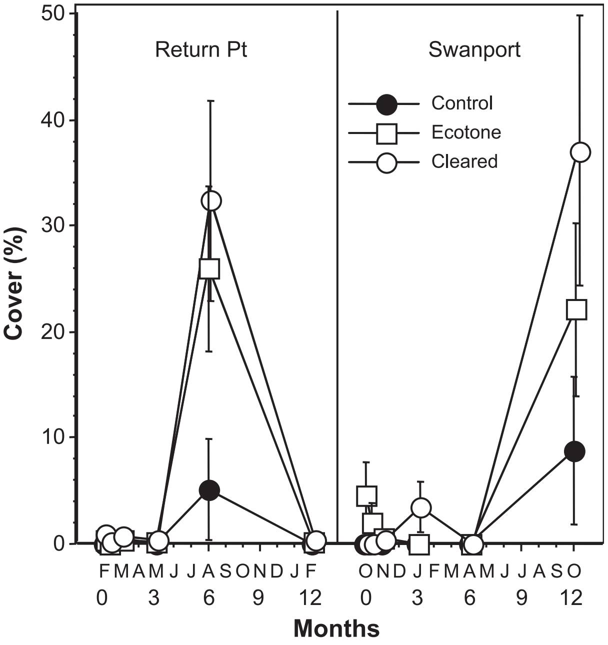

Fig. 6. Mean changes in cover (±S.E.) of the introduced kelp *U. pinnatifida* during the year following macroalgal removal from 50×12-m blocks at two sites where present. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

for the three particular sites examined, rather than a significant effect spanning the region.

Variates found to be significantly affected by algal clearance were examined graphically. In order to assess whether any species was associated directly with the ecotonal interface at the edge of cleared blocks rather than open areas, data presented in figures have been separated into three rather than two treatment categories—'cleared' (30-m transect block at the centre of each clearing), 'control' (30-m transect block at the centre of each undisturbed block), and 'ecotone' (mean of data collected within 10 m of a clearing boundary).

3. Results

3.1. Changes in density following algal clearance

Changes in algal assemblages over the 12-month period following plant clearance are shown as MDS plots for the three sites in Fig. 1. Algal assemblages at all sites were extremely diverse, with a total of 74 plant species possessing >5% cover in a quadrat recorded. Different macroalgal species dominated different sites, hence variation between

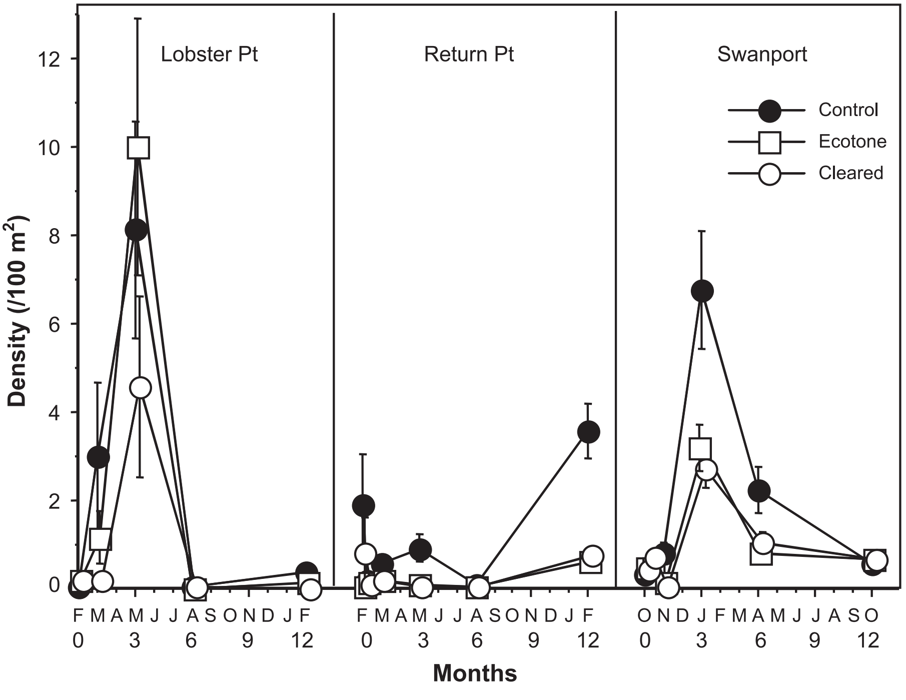

Fig. 7. Mean changes in density (±S.E.) of *A. vittiger* during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

sites was much greater than that associated with experimental treatments. Within sites, macroalgal assemblages changed little through the year for control blocks but exhibited a major change immediately after macroalgal clearance in manipulated blocks, returning to near control values after 12 months.

Fish assemblages generally showed comparable biotic patterns between sites, times and treatments as for plant assemblages, but with some differences in magnitude. Sites possessed lower biotic distinctiveness for fishes than for plants; seasonal variation for fishes was greater than observed for plants; and a higher level of overlap was evident between treatment and control blocks, particularly for the Return Point site (Fig. 1).

Invertebrate assemblages were highly localised with respect to site. Patterns in control blocks over time were almost identical to those in clearance blocks, with the exception of Lobster Point (Fig. 1). Stress values associated with all three plots were low (<0.15), indicating that the figures provide good representations of biotic patterns.

The effect of macroalgal clearance on abundance of common species and species richness of fish, invertebrate and macroalgae was assessed using repeated-measure ANOVAs, with results presented in Tables 1, 2 and 3. With respect to effects of algal clearance on the biotic community, the factors of main interest amongst the ANOVA output were ‘clearance’ and its interactions.

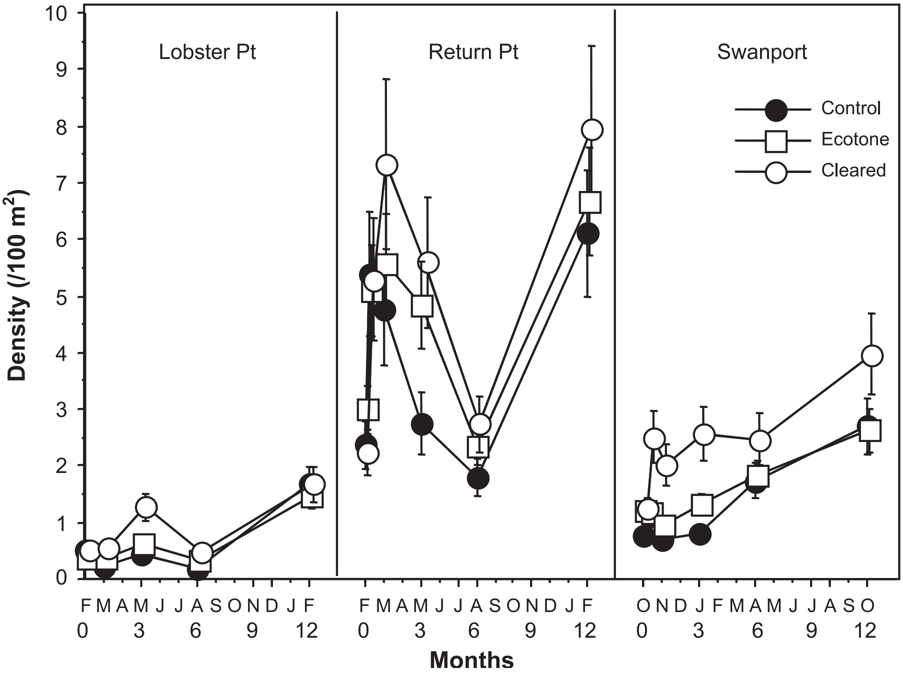

Fig. 8. Mean changes in density (±S.E.) of *N. tetricus* during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

Total algal cover and 'kelp' cover (sensu laminarian plus fucoid algae) both generated significant 'clearance' and 'occasion*clearance' terms in the ANOVA (Table 1), the expected outcome given that these factors were directly manipulated by divers during canopy clearance and partially recovered during the 1-year course of the experiment. Algal species richness was also associated with significant 'clearance' and 'occasion*clearance' effects, but only when site was considered a fixed factor in the ANOVA model (Table 1). This more restrictive model relates to the specific case of the three investigated sites only.

Total algal cover declined from ≈ 120% to ≈ 40% following canopy removal (Fig. 2), whereas 'kelp' cover declined from ≈ 100% to ≈ 6% (Fig. 3). By the end of the 12-month experiment, 'kelp' cover had recovered to half initial values at Return Point and Little Swanport, and one-third initial values at Lobster Point. 'Kelp' cover in control blocks notably declined to half initial values at Little Swanport during the 12-month course of the experiment. Following canopy removal, the total number of algal species per quadrat declined by 3 at Return Point and 1 at Lobster Point and Little Swanport, with recovery to initial values within 12 months at all sites (Fig. 4).

Amongst the algal taxa that comprised the category 'kelp', recovery of stringy fucoids in the genera *Cystophora* and *Sargassum* was considerably more rapid than for the laminarians *E. radiata* and *M. pyrifera*, or the massive flat-branched fucoid *P. comosa*. After 12 months, species of *Cystophora* and *Sargassum* amalgamated as a

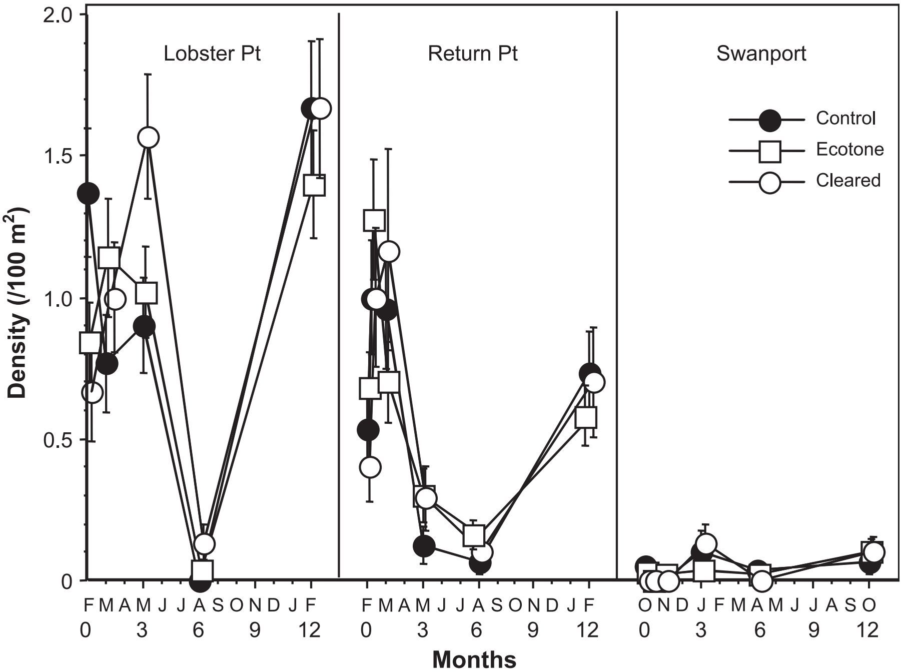

Fig. 9. Mean changes in density (±S.E.) of *P. laticlavius* during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

group had recovered to 36%, 62% and 46% of initial values in cleared patches at Lobster Point, Return Point and Little Swanport, respectively. By contrast, neither *M. pyrifera* nor *P. comosa* plants were recorded after 12 months at Little Swanport—the only site where they were initially present. These two species possessed 32% and 56% cover, respectively, at the start of the experiment. *E. radiata* was not recorded in cleared patches after 12 months at Return Point, albeit possessing a low initial cover (6%), but at the other site where it was present (Lobster Point), this alga recovered to 30% of initial values in cleared patches.

None of the turfing algae showed a consistent response to the habitat manipulation, including *Caulerpa* spp., branched coralline algae, and foliose red algae, when species belonging to these groups were aggregated. *Caulerpa* spp. possessed a significant 'occasion*site*clearance' interaction; however, inspection of data (Fig. 5) indicated that this outcome resulted more from changes over time in control blocks than canopy removal blocks, and that changes were inconsistent between sites and also for each of the eight different *Caulerpa* species recorded during the study. This significant result was possibly a Type II statistical error resulting from the large number of tests made.

The introduced laminarian kelp *Undaria pinnatifida* exhibited major changes following habitat manipulation (Table 1, Fig. 6). For the two sites investigated within the current

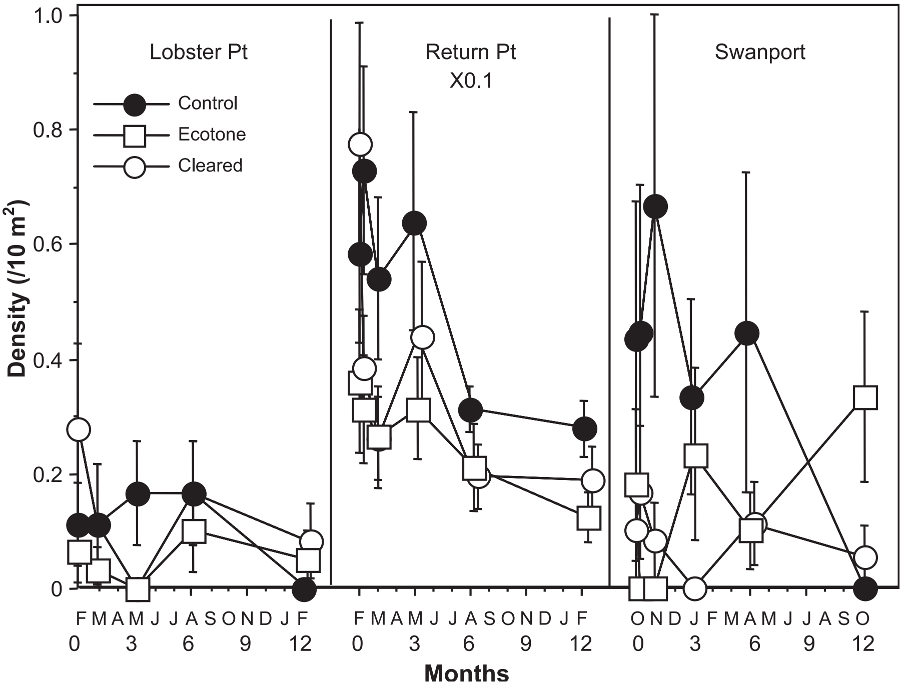

Fig. 10. Mean changes over time in density (±S.E.) of *H. ruber* during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

range of this plant, *U. pinnatifida* increased in density to cover ≈35% of reef substrata in cleared blocks during the sporophyte growing season, whereas in control blocks cover was only ≈7%. *U. pinnatifida* is an annual species, developing largest sporophytes during late spring, a season that coincided with the 6-month sampling occasion at Return Point and 12-month sampling occasion at Little Swanport.

Common fish species affected by algal clearance, as indicated by significant 'clearance' or 'site*clearance' terms in the ANOVA (Table 2), comprised *Notolabrus tetricus*, *Acanthaluteres vittiger* and *Pictilabrus laticlavius*. The monacanthid *A. vittiger* was consistently less abundant in cleared blocks compared to control blocks (Fig. 7), whereas the wrasses *N. tetricus* (Fig. 8) and *P. laticlavius* (Fig. 9) showed the opposite response. Densities of the majority of fish species changed significantly between sampling occasions (Table 2).

Macroinvertebrate taxa and cryptic fishes showed little response to habitat manipulation, other than the abalone *Haliotis ruber* and the sea urchin *Heliocidaris erythrogramma* (Table 3). Densities of both herbivorous species fell to approximately half control densities in cleared blocks (Figs. 10 and 11), with this decline occurring during the month following canopy removal. Densities of the third herbivorous species that occurs commonly in the study region—the gastropod *Turbo undulatus*—declined to a comparable extent (Fig. 12); however, in this case changes were not significant at the 5%

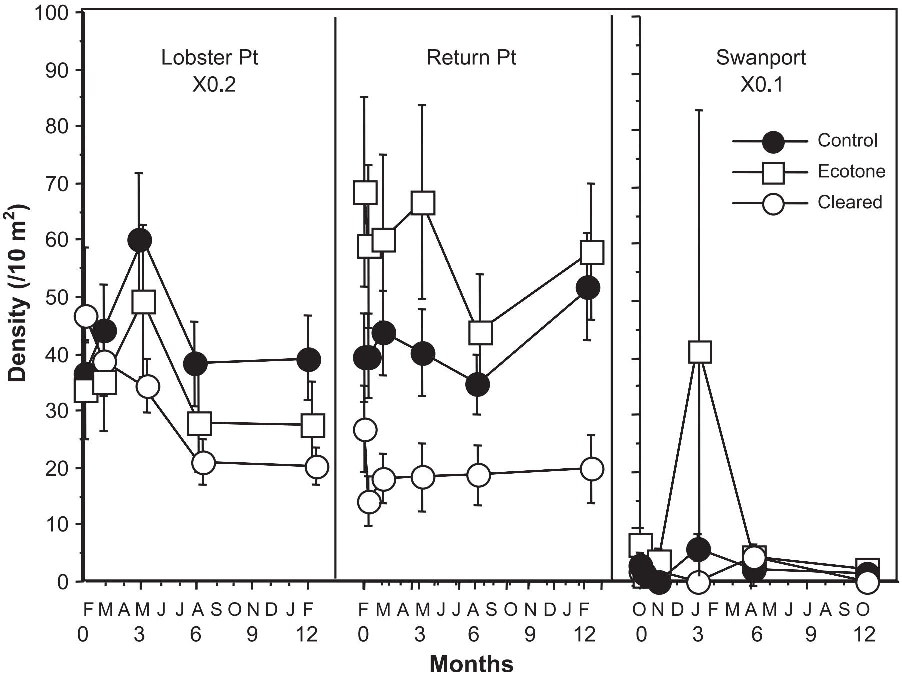

Fig. 11. Mean changes over time in density (±S.E.) of *H. erythrogramma* during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

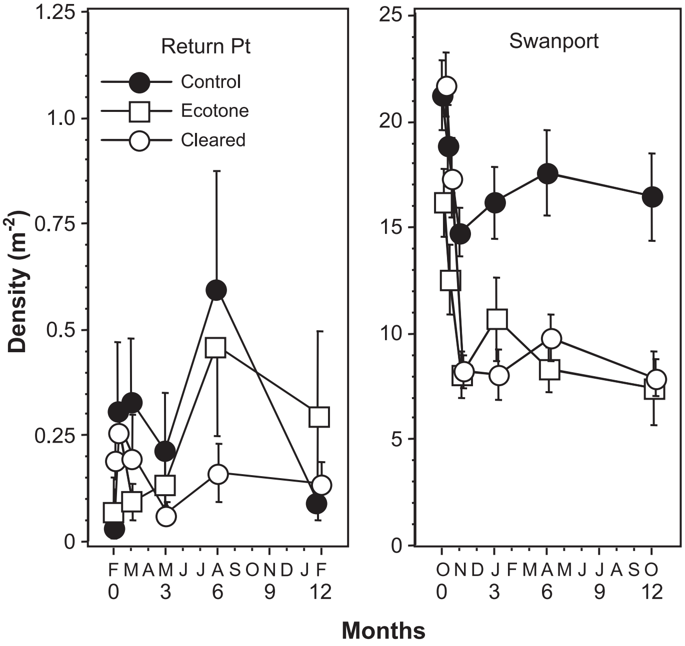

Fig. 12. Mean changes over time in density (±S.E.) of *T. undulatus* during the year following macroalgal removal from 50×12-m blocks at three sites. Data were categorised as belonging to the central 30-m region of cleared or control blocks, or at the ecotone (<10 m from the clearing boundary).

level (p=0.09), even when considering site a fixed factor in the ANOVA model, perhaps because a clumped distribution added considerable stochastic error.

None of the common fish or invertebrate species investigated exhibited a consistent association with the ecotonal edge of cleared patches.

4. Discussion

4.1. Effects of canopy clearance on the reef flora

Given the reported magnitude of community-level transformation associated with barrens formation, and outcomes of clearance experiments elsewhere (Fletcher, 1987; Kennelly and Underwood, 1993; Benedetti-Cecchi et al., 2001; Melville and Connell, 2001), unexpectedly little change in algal populations was detected in our study following canopy removal. Other than for species directly manipulated by divers and the introduced kelp *U. pinnatifida*, no consistent change was detected amongst plant species in experiments.

Thus, turfing algae, including *Caulerpa* spp., foliose rhodophytes and articulated corallines, were not consistently affected by canopy removal, either positively in response to factors such as increased light or water flow, or negatively in response to increased UV irradiation or wave turbulence at the seabed. By comparison, removal of the algal canopy in Mediterranean experiments led to a more than threefold increase in cover of both articulated corallines and ‘coarsely branched’ algae (Benedetti-Cecchi et al., 2001).

Our anomalous results are unlikely to be related to the large size of our clearance plots (600 m^2 cf. 1–5 m^2 in experiments by authors cited above). Most effects should be magnified in large clearings because the physical environment is less affected by influences of nearby vegetation than in small clearings. Edge effects, which disproportionately affect small patches, were not detected. Near clearing boundaries, densities of common fish and invertebrate as well as algal species were generally intermediate to those found in cleared and control blocks.

The poor response amongst algal taxa in our clearance experiments may be related to kelp density (Melville and Connell, 2001); however, this is unlikely given that the cover of laminarian and fucoid algae at the start of experiments was close to 100% (Fig. 3). While not measured here, total algal biomass was moderately high and comparable to the mean dry weight of 400 g/m^2 recorded in the same region by Edgar (1983a,b). Turfing algae should respond more readily to removal of a dense algal canopy than a sparse canopy because a dense canopy reduces light and water motion to a greater extent.

Alternatively, the abundance of stringy fucoid algae at our study sites, as opposed to the laminarian kelps with flat thalli generally studied elsewhere, may have allowed considerable light to penetrate the canopy in control plots and reach the understory layer. We regard this hypothesis also as unlikely given that Benedetti-Cecchi et al. (2001) found changes in numerous algal taxa within 4 months following clearance of stringy *Cystoseira* spp. on northern Italian reefs.

The most likely reason for the poor turfing algal response in our experiments is that the canopy represented a mosaic of species interspersed with turfing algae rather than a monospecific canopy overlying coralline-algal-encrusted rock, as described in most other studies. The diversity of macroalgae was high at our study sites, as was the level of macrophytic cover remaining ($\approx$40%) after canopy removal. Moreover, fucoid algae recovered rapidly in cleared blocks. Hence, although our cleared patches showed similarity to urchin barrens in lacking canopy algae, they differed in terms of considerable biomass of persistent turfing macroalgae.

Outcomes of our experiment were consistent with concurrent field manipulations undertaken independently with smaller clearance areas (16 m^2) at a site 10 km south of Little Swanport (Valentine and Johnson, 2003). In all Tasmanian experiments, stringy fucoid algae belonging to the genera *Cystophora* and *Sargassum* recovered in cleared patches more rapidly than laminarian algae (*E. radiata* and *M. pyrifera*) and fucoid algae with broad-thalli (*P. comosa*, *Carpoglossum confluens* and *Seiroccoccus axillaris*). These patterns were evident despite experiments being affected by an anomalously hot summer and autumn in early 2001 that caused extensive regional mortality of broad-thallus kelp plants, particularly within our control plots at Little Swanport (Fig. 4). Longer-term experimentation is required to assess whether recovery of broad-thallus algae occurs more rapidly during ‘normal’ years than in our experiments, and also whether larger broad-thallus algae eventually exclude stringy fucoids after clearance or are disadvantaged by their presence.

The one striking change following algal manipulation in our experiments was the seasonal predominance of *U. pinnatifida* in cleared patches. This introduced kelp preferentially develops in urchin barren grounds along the Tasmanian east coast (Valentine and Johnson, 2003), as well as within cleared areas in our experiments. *U. pinnatifida* is an annual species that apparently cannot compete well with large perennial brown algae, and is inhibited from establishing dense populations amongst natural kelp beds (Valentine and Johnson, 2003). However, spores that settle in cleared patches and barren grounds are able to develop to a large size during the spring sporophyte growing season.

The dependence of *U. pinnatifida* on open reef space, particularly sea urchin barrens, implies that population density of this kelp is probably mediated in part by fishing of urchin predators. Exclusion of fishers from urchin barren habitat within a marine reserve at Leigh, New Zealand, resulted in habitat transformation to fucoid algal beds following a build-up in densities of urchin predators (Babcock et al., 1999; Shears and Babcock, 2002; Shears and Babcock, 2003). Also, ongoing monitoring of the 'no-take' Maria Island marine reserve, which extends north of our Return Point study site, has shown an order of magnitude increase in biomass of rock lobster predators within the reserve (Edgar and Barrett, 1999), and a significant decline in grazing urchin and abalone densities after 10 years of protection (Barrett and Edgar, unpublished data).

Thus, adequately enforced marine reserves in eastern Tasmania are likely to retard propagation of *U. pinnatifida* beds because the presence of numerous rock lobster and predatory fishes will exert greater control on urchin numbers, inhibiting barrens formation. MPAs elsewhere may also assist benthic communities resist invasion by exotic species. In general, assemblages stressed by human impacts tend to show less resistance to invasion than undisturbed assemblages (Nichols et al., 1990; Lodge, 1993; Moyle and Light, 1996; D'Antonio et al., 1999; Reusch and Williams, 1999), and fishing comprises one form of anthropogenic stress.

4.2. Effects of canopy clearance on the reef fauna

Results of MDS indicate that the macroinvertebrate assemblage exhibited less response to canopy clearance than the plant and fish communities. Most macroinvertebrate taxa are probably primarily associating with the turfing algal layer or seabed rather than with canopy plants.

Amongst the common invertebrate species, the grazing urchin *H. erythrogramma* and abalone *H. ruber*, and probably also the gastropod *T. undulatus*, exhibited population declines in the month following canopy removal. Predation was probably responsible for these declines. Many broken *Turbo* shells were observed on the seabed during the week following algal clearance, as were numerous shells of recently dead abalone.

As in other studies (Ebeling and Laur, 1985; Ebling et al., 1985; Carr, 1989; DeMartini and Roberts, 1990), changes in fish populations were detected following algal canopy clearance. Changes observed following manipulation may have resulted from direct associations between fishes and plants, both positive and negative, or may represent sampling artefacts caused by greater diver detectability of fishes in areas lacking dense algal cover.

The two fishes exhibiting clearest observed changes following algal clearance were the wrasse *N. tetricus*, which doubled in abundance in cleared blocks (Fig. 4), and the monacanthid *A. vittiger*, which halved in numbers following algal manipulation. In concurrent trapping experiments, *N. tetricus* was not caught in fish traps in proportionately higher numbers within cleared blocks (Edgar et al., 2004). Thus, the most likely cause of the higher numbers of *N. tetricus* observed during visual transects was that animals were increasingly visible to divers in open areas rather than that they had immigrated into the cleared blocks.

The response of *A. vittiger* to algal removal was more direct, representing a preference for densely vegetated habitats. Fish trap data revealed a decline in *A. vittiger* numbers in cleared blocks (Edgar et al., 2004), and declines in density were also found in a Victorian clearance study involving the same species (Jones, 1992). Personal observations indicate that the species feeds on epifaunal invertebrates and filamentous epiphytes amongst the algal canopy at sites studied.

In addition to providing protection from predators (Guidetti, 2000), the presence of a dense plant canopy probably supports many fish populations in kelp forests through the productivity of associated food resources. Densities of small ‘mesograzers’, such as amphipods, polychaetes and gastropods, provide the bulk of the diets of the majority of small demersal fishes in vegetated habitats (Edgar and Shaw, 1995). Mesograzers can occur in tens of thousands per square metre amongst Tasmanian seaweeds (Edgar, 1983a,b), and are likely to be at least an order of magnitude more abundant in kelp forests than open barren grounds.

Conversely, some fish species are negatively affected by the presence of dense kelp (Jones, 1992; McClanahan et al., 1999). Across southern Australia, fish communities associated with urchin barrens generally tend to be dominated by planktivorous and omnivorous species, whereas carnivores that consume mesograzers and herbivores more typically predominate in kelp-dominated habitat and near ecotones (Edgar and Barrett, unpublished data). Given the extent to which canopy loss affects many fish species, any consideration of ecosystem changes that accompany transformation of vegetated areas to urchin barrens should include an assessment of changes to associated fish populations, as well as the more readily documented changes to plants and invertebrates.

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