

Patch formation by herbivorous fish in a temperate Australian kelp forest

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Summary. The odacid fish *Odax cyanomelas* feeds on the kelp *Ecklonia radiata*, an important component of subtidal reef habitats on the central coast of New South Wales, Australia. Herbivory by *Odax* has a major impact on the structure and dynamics of discrete patches within larger stands of kelp at Cape Banks. This three-year study showed that each year, between August and October, approximately the same patches of kelp were denuded by preferential feeding on the meristem and primary laminae. This coincided with a variable pulse of *Ecklonia* recruits to the cleared patches, thereby generating patches of a single age-class of plants. Neighbouring areas of *Ecklonia* forest, non cleared by *Odax*, consisted of larger, perennial plants, which exhibited more gradual changes in abundance. The seasonal impact of *Odax* appeared to be due to a change in the behaviour of female *Odax* during their spawning period. Observations suggested that females aggregate at traditional sites prior to spawning with territorial males in adjacent areas of kelp forest. An alternative hypothesis, that *Odax* preferentially attacked stands of one-year old *Ecklonia* plants, was rejected by a field experiment; the establishment of experimental stands of one-year old plants did not lead to increased damage due to *Odax* or any change in the use of space by the fish. The generality of this effect of fish herbivory is unknown, but this and other *Odax* species are widely distributed throughout temperate Australia, where *Ecklonia* is the dominant laminarian alga. The effects of pulsed herbivory by *Odax* is contrasted to the more continuous grazing by sea urchins in the same system. The latter herbivore has been shown to maintain areas free of *Ecklonia*, the long-term effects of herbivory by *Odax* remain unclear.

Key words: Herbivory – Fish – *Odax cyanomelas* – *Ecklonia radiata* – Australia

Attention to the processes that introduce spatial and temporal heterogeneity to the structure of habitats is increasing (see Sousa 1984; Pickett and White 1985). The scales over which heterogeneity in habitat structure occurs directly influence how assemblages, populations and individuals respond to their environment (Wiens and Rotenberry 1981; Auerbach and Shmida 1987; Choat and Ayling 1987; Morris 1987). Patchy or complex environments promote diversity by enhancing the recruitment and persistence of species with differing resource requirements (Ricklefs 1977; Heck and Orth 1980; Lubchenco and Gaines 1981; Tonn and Magnuson 1982). Habitat complexity may affect the outcome of potentially important processes such as competition and predation (Atkinson and Shorrocks 1981; Peterson 1982; Gaines 1985) and directly influence behavioural decisions related to foraging and predator avoidance (Harrold and Reed 1985; Wiens 1985; Holbrook and Schmitt 1988). Despite their potentially far-reaching effects, the processes establishing and maintaining discontinuities in habitat structure are often little understood.

Spatial and temporal patchiness in habitat structure appears to be characteristic of shallow, hard substratum communities in temperate waters (Dayton et al. 1984; Keough 1984; Dayton and Tegner 1984). Recent reviews indicate substantial gaps in our knowledge with respect to the creation and dynamics of these patches (Dayton 1985; Connell and Keough 1985; Sousa 1985). Kelp forests, which dominate rocky reef habitats in temperate regions (Dayton 1985; Schiel and Foster 1986; Schiel 1988) are a case in point. Patches exist in the form of monospecific or mixed stands of foliose algae, urchin-grazed sites and areas covered in low turfing algae (see

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above references). The creation of patches in kelp forests has primarily been attributed to physical disturbance (Dayton and Tegner 1984; Harris et al. 1984; Kennelly 1987a, b, c) and the localized action of echinoid grazers (Chapman 1981; Andrew and Choat 1982; Cowen et al. 1982; Harrold and Reed 1985; Fletcher 1987).

Herbivorous fish can be abundant in temperate rocky-reef habitats (Choat 1982; Jones 1988), but few workers have examined the effects of these fishes on the structure of these communities (but see Horn 1983; Harris et al. 1984). This stands in sharp contrast to the voluminous literature on herbivorous fish associated with coral reefs, where, in the absence of kelp, they appear to have a major impact on the abundance of algae (e.g. Hay 1981, 1984; Sammarco 1983; Carpenter 1986; Lewis 1986; Scott and Russ 1987).

This study was prompted by the observation, in October 1985, of gaps 1–100 m² in area appearing in the canopy of forests of the laminarian alga *Ecklonia radiata* (C Agardh) J. Agardh (hereafter *Ecklonia*) in central New South Wales. The laminae of plants were observed to have been removed by a herbivore biting away the meristematic tissue at the base of the primary lamina, often leaving only the holdfast, stipe, and the remnants of primary meristem. Bite marks in the primary lamina were diagnosed as belonging to the herbivorous fish *Odax cyanomelas* (Richardson) and were clearly distinguishable from those made by other herbivores such as sea urchins. The genus *Odax* is endemic to temperate Australasia (Gomon and Paxton 1985).

The aim of this study was to describe the formation and dynamics of patches caused by *Odax cyanomelas* (hereafter *Odax*). We examined temporal changes in abundance of the species in areas subject to *Odax* feeding and in adjacent, undisturbed, areas over three years. Direct observations of the foraging behaviour of *Odax* confirmed their role in patch formation and indicated that *Odax* cleared patches in the same places at the same times each year. Hypotheses to explain this apparent preference for particular patches were tested by experiment.

Formation of patches in *Ecklonia* forests

Study area

The study was done in a region of shallow (<10 m) rocky reef at Cape Banks, near Sydney, New South Wales. This heterogeneous area of reef consists of a variety of habitat types ranging from dense canopy-forming *Ecklonia* forests to areas of reef devoid of foliose algae and supporting high densities of invertebrate herbivores such as limpets and sea urchins (Fletcher 1987; Andrew and Underwood 1989).

Methods

The percentage cover of cleared forest at each site was estimated by five replicate line transects laid out during October 1986, during

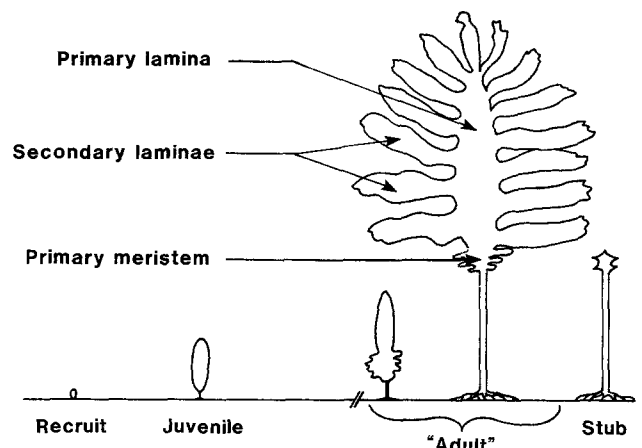


Fig. 1. Terminology used to describe different age and damage categories of *Ecklonia radiata*

a period of severe *Odax* damage. In each of the 50 m transects the proportion of cleared forest that intersected with the tape was recorded. In areas of forest that had been cleared, there were large numbers of stubs, all bearing the diagnostic bite marks made by *Odax*.

Ten permanent 1 m² quadrats were established in areas of *Ecklonia* forest not cleared by the fish. These quadrats were set up at Site 1, where grazing by *Odax* was first observed. The densities of *Ecklonia*, invertebrate herbivores and several species of understory algae were estimated bimonthly (more frequently in spring) between October 1985 and January 1988. Three ontogenetic stages were recognized in *Ecklonia* (Fig. 1): (1) recruits—very small plants (<30 mm long) usually less than 1 month old and with no visible stipe, (2) juveniles—plants with a visible stipe, a primary lamina but no secondary lamina, and (3) adults—plants old enough to have secondary laminae branching off the primary lamina. The term 'adults' is used loosely and does not necessarily reflect the reproductive condition of plants.

In October 1985 ten plants from which all but the basal meristematic tissue (Fig. 1) had been removed by *Odax* ('stubs') were tagged in each of eight permanent quadrats in order to monitor the ability of those plants to reestablish themselves ($n=80$). These plants were followed through time until they disappeared. All but 3 of these plants (3.8%) had disappeared by April 1986, and by July 1986 all of the tagged plants had died. None of the plants regrew laminae.

Results

The percentage of kelp forest cleared by *Odax*, as evidenced by large numbers of stubs with diagnostic bite marks, was similar, and substantial at all three sites as surveyed at Cape Banks in October 1986 (Site 1: 36.8%, SE=9.1, Site 2: 34.4% \pm 9.7, and Site 3: 23.0% \pm 7.9).

There were substantial differences in the patterns of change in the density of adult *Ecklonia* between those areas damaged by *Odax* and those that were undamaged (Fig. 2A). In damaged areas (hereafter termed 'patch') the density of adult *Ecklonia* varied widely, whereas in undamaged areas ('forest'), the density of adult plants underwent a gradual decline. The density of adult *Ecklonia* in the 'patch' quadrats prior to their clearance in 1985 was estimated by back-calculating from the number of stubs and stipes found in October 1985. This

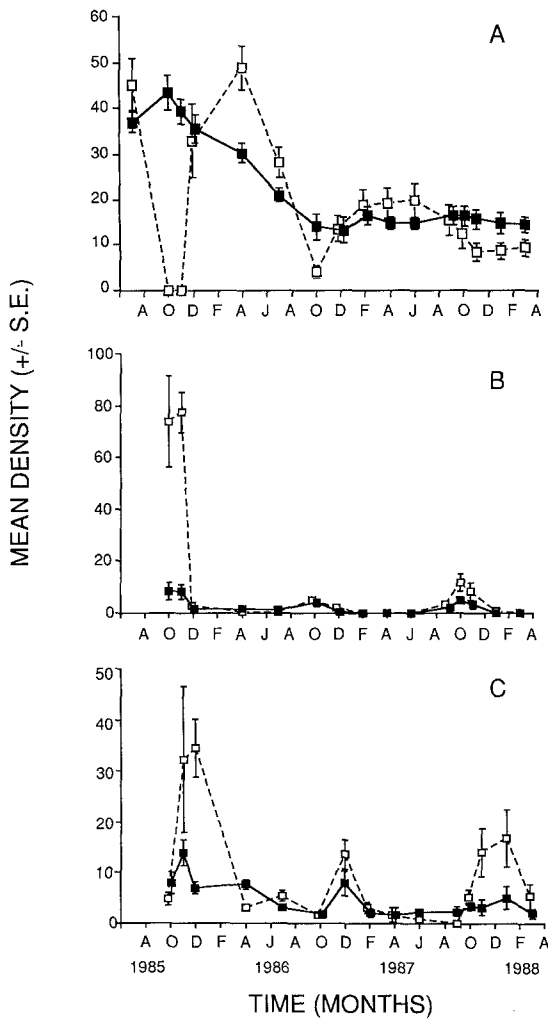


Fig. 2A-C. Patterns of change through time in the density of A Adult B Recruit, and C Juvenile *Ecklonia radiata* in 'patch' (□) and 'forest' (■) quadrats. Data per 1 m², n=10

estimate must be regarded as a minimum as some stubs or stipes may have been dislodged prior to sampling in October. The density of adult *Ecklonia* declined rapidly between August-October 1985 (Fig. 2A). This pattern was repeated, though less dramatically, in spring of the two subsequent years. The density of adult plants in late spring of each year, at the time of greatest activity by *Odax*, was significantly lower (October 1986: $t_{(18)}=2.84$, two tailed $P<0.05$, November 1987: $t_{(18)}=2.34$, $P<0.05$) than in those quadrats within areas that were not deforested in 1985.

The density of adult *Ecklonia* in the 'patch' quadrats increased in summer of the first two years as juveniles grew into the class designated as adults (Fig. 2A). The density of adult *Ecklonia* did not recover following clearances in 1987 but remained at approximately 15 m⁻² (Fig. 2A). There was a net decrease in the density of adult *Ecklonia* in the 'patch' quadrats over the period October 1985 to January 1988 (Fig. 2A). There was also a decline in the density of adult plants in the 'forest' quadrats during the study, although the decrease in density in these quadrats was considerably more monotonic than in the 'patch' quadrats (Fig. 2A).

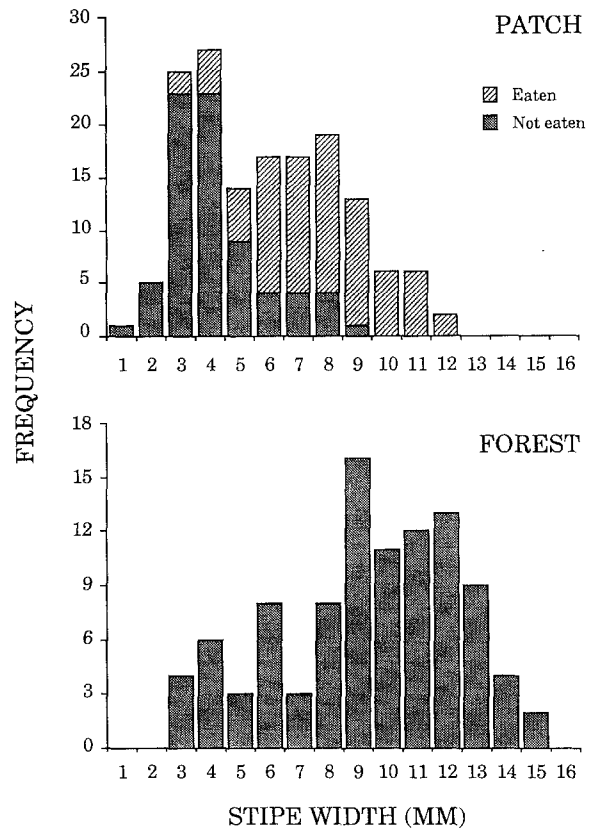


Fig. 3. Size-frequency distribution of *Ecklonia* plants from 'patch' (*Odax*-damaged, n=150) and 'forest' (undamaged, n=100) quadrats during October 1987. In 'patch' quadrats, damaged and undamaged plants are distinguished

Ecklonia recruited in spring of each year (Fig. 2B). The mean density of recruits in the 'patch' quadrats in October 1985 was very high (73.9 SE=17.6, n=10) and significantly greater ($t_{(18)}=3.65$, $P<0.01$) than in the 'forest' quadrats (8.5 +/- 3.3). Recruitment of this magnitude to the 'patch' quadrats was not repeated in subsequent years and there was no significant difference in the density of recruits between 'forest' and 'patch' quadrats in either October 1986 ($t_{(18)}=0.64$, n.s.) or October 1987 ($t_{(18)}=1.87$, n.s.).

The density of juvenile plants increased in the months following the appearance of the recruits as individuals grew and developed visible stipes (Fig. 2c). There was a significant difference in the density of juveniles between 'patch' and 'forest' quadrats only in December 1985 ($t_{(18)}=4.71$, $P<0.001$). No significant difference in the density of juveniles between the 'patch' and 'forest' quadrats was found in December 1986 ($t_{(18)}=1.55$, n.s.), or January 1988 ($t_{(18)}=1.96$, n.s.). Differences in the peak density of juveniles among years reflected patterns in recruitment. That is, the density of juveniles in 'patch' quadrats was considerably larger in 1985 than it was in 1986 and 1987 (Fig. 2c).

There were clear differences in the size structure of plants in the 'patch' and 'forest' quadrats in October 1987 (Fig. 3). At this time, the mean stipe diameter of plants in 'patch' quadrats (5.9 mm SE=0.2, n=150) was significantly less ($t_{(148)}=9.78$, $P<0.001$) than in the 'for-

est' quadrats (9.4 ± 0.3 , $n=100$). Within 'patch' quadrats there were differences in the size of *Odax*-damaged and undamaged plants. The mean stipe diameter of plants with at least one bite mark ($7.5 \text{ mm} \pm 0.2$) was significantly larger than the mean for ungrazed plants (4.2 ± 0.2 , $t_{(148)}=11.85$, $P<0.001$). None of the plants measured in areas of *Ecklonia* forest had been damaged to the extent that all of their primary laminae had been removed.

'Patch' and 'forest' quadrats developed differences in the mean densities of macro-algal species not eaten by *Odax* (Fig. 4). The mean abundance of *Sargassum* spp. (primarily *S. lineariaefolium*) was consistently higher in undamaged areas (Fig. 4A), whereas sub-canopy algae such as *Zonaria* spp. and *Dellisea pulchra* (Grev.) Mont., were more abundant in the *Odax*-cleared quadrats (Fig. 4B). There was a net increase in the combined mean density of *Zonaria* spp. and *D. pulchra* in both the 'forest' and 'patch' quadrats over the period of the study (Fig. 4B). The rise in mean density of these species was greatest in spring and early-summer of each year (Fig. 4B). The combined density of the large gastropod

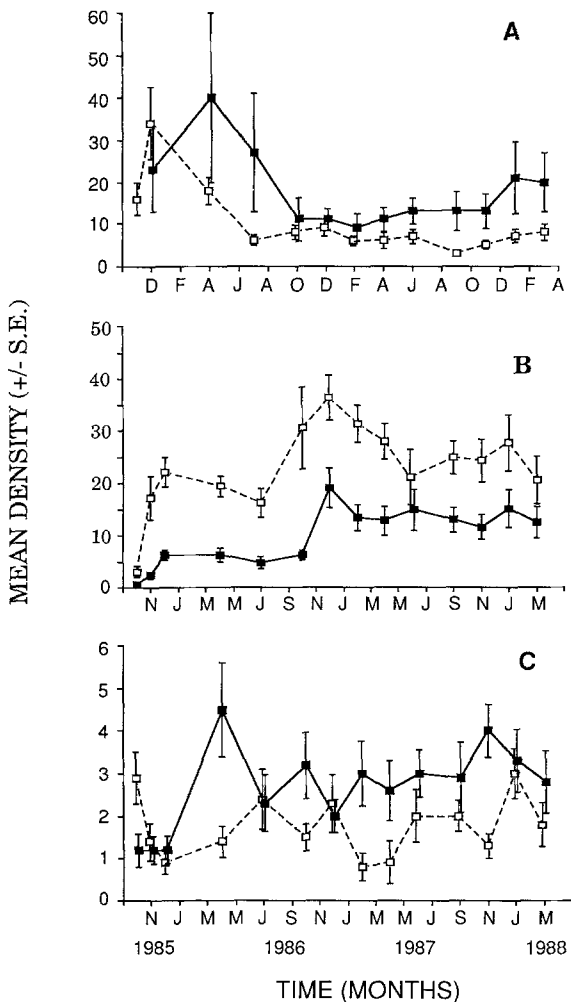


Fig. 4A–C. Temporal changes in the densities of A *Sargassum* spp., B Combined density of *Zonaria* spp. and *Dellisea pulchra*, C Combined density of *Australium tentiforme* and *Turbo torquata*, in 'patch' (□) and 'forest' (■) quadrats

grazers *Australium tentiforme* (Menke) and *Turbo torquata* (Gmelin) exhibited irregular changes although there was some indication that numbers were, on average, greater in 'forest' areas (Fig. 4C).

Abundance and behaviour of *Odax cyanomelas*

Methods

The study area at Site 1 was mapped by marking the perimeter of the kelp forest, obvious topographic features and regions of patch formation (Fig. 5). Observations of the foraging behaviour of *Odax* and their use of space were made during August/September 1987, a period when clearances were being expanded. This was done to establish whether *Odax* consumed *Ecklonia* and were responsible for a creation of patches, and to determine how the locations of patches related to the dispersion and movements of fish. The sexes exhibited distinct differences in colour (males – black with iridescent blue markings on the caudal fin; females – brown, mottled), allowing them to be separated for observation. Males could further be separated by unique patterns to their bright blue markings on the caudal fin. Six individuals of each sex were collected from a nearby reef to support feeding observations with an examination of stomach contents.

Individually recognized males and randomly selected females were observed for 15-min periods. The location and number of feeding bites were recorded within 'patch' (< 1 m from cleared area) and 'forest' areas. Bites on *Ecklonia* were separated into those made on the meristem (at the base of the primary lamina) and on the lamina. Bites made on the primary and secondary laminae could not be separated because of the secretive nature of the fish. The males were observed for 7.25 h and the females for 5.5 h during the daylight hours over a 2-week period during August/September 1987.

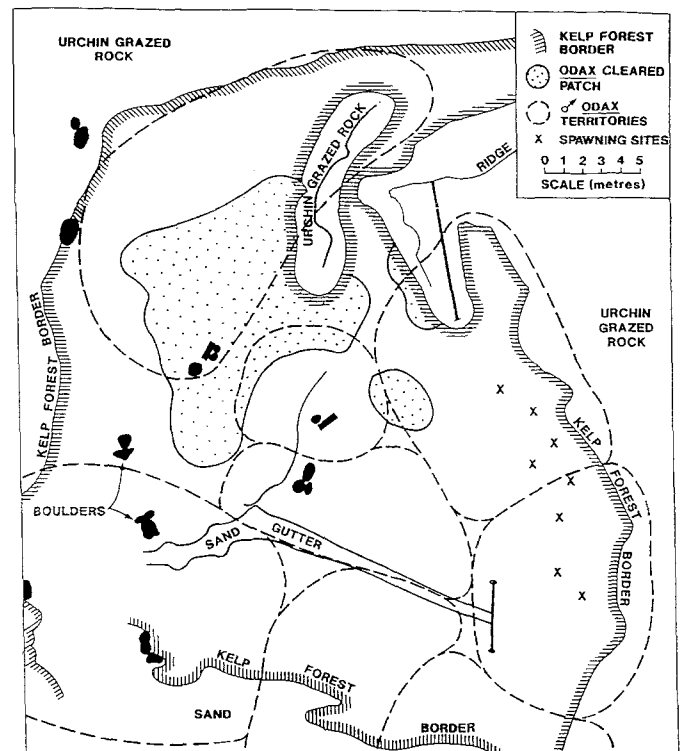


Fig. 5. Map of Site 1 made during August/September 1987, showing the border of the kelp forest, *Odax*-cleared patches, the territories of individual male *Odax* and locations of observed spawnings

Ten males resided in the study area and all exhibited conspicuous aggressive behaviour. Repeated observations were made on the same individuals, recording their movements, and the areal extent of individual territories. The densities of male and female *Odax* at each of the three sites were estimated at three times (October 1986, May 1987, and July 1987) by making visual counts in five 25 × 5 m transects placed randomly within each site.

Prior to analysis of variance, heterogeneity of variance, as indicated by Cochran's test (Winer 1971), was stabilized by transformation and these are indicated where appropriate. Ryan's test was used to distinguish among means following analysis of variance (Day and Quinn 1989). In all cases the tests gave logical results and these are summarised in the text. Unless otherwise stated, significance levels are set at $P < 0.05$.

Results

Behavioural observations in spring 1987 indicated that both male and female *Odax* fed almost exclusively on *Ecklonia*. This was confirmed by examination of the stomach contents of 12 individuals collected from a nearby reef area which contained greater than 99% (by volume) *Ecklonia* in all cases. Although male and female *Odax* consumed the same food, however, there were substantial differences in their foraging behaviour. Feeding by females was concentrated in 'patch' areas (Table 1) which were being enlarged. Approximately 10% of bites observed in 'patch' areas were taken from the meristem of plants. Removal of the meristematic tissue can essentially "decapitate" a plant without the laminae being consumed. Feeding rates of males were, on average, considerably less than females and all bites were taken from the laminae of plants in forested areas outside the clearances (Table 1).

While females were aggregated in areas of forest being cleared, males were spaced apart (Fig. 5) and highly aggressive toward one another. Most of the kelp stand at Site 1 was occupied by territorial males. Females were frequently courted and chased by males. All recorded spawnings occurring near the deeper edge of the kelp forest (Fig. 5).

The densities of male *Odax* at Site 1 were similar to the other two sites surveyed, and sampling at three times suggested relatively constant densities (Table 2). There were no significant differences in the density of male *Odax* among sites ($F_{(2,4)} = 3.5$, n.s.) or times ($F_{(2,4)} = 3.3$, n.s.). Female densities also did not differ significantly between times ($F_{(2,4)} = 0.5$, n.s., square-root

Table 1. Mean number (+/- SE) of feeding bites made by male and female *Odax* observed for 15 min periods in September 1987. Bites are partitioned into those made in 'patch' and 'forest' areas, and those taken from the meristem and laminae portions of plants (males: $n = 29$, females: $n = 22$)

		Males	Females
Patch:	Lamina	~0	18.3 +/- 2.0
	Meristem	~0	2.1 +/- 0.6
Forest:	Lamina	11.0 +/- 1.1	1.4 +/- 0.5
	Meristem	~0	~0

~0 indicates less than 0.05

Table 2. Densities of male and female *Odax* (per 125 m² $n = 5$, +/- SE) at the three sites, surveyed at three randomly chosen times

	17 October 1986	31 May 1987	18 July 1987
Males:			
Site 1	2.0 + 0.9	0.8 + 0.3	1.6 + 0.5
Site 2	1.4 + 0.5	0.6 + 0.5	1.4 + 0.5
Site 3	2.6 + 0.6	1.2 + 0.2	4.6 + 0.6
Females:			
Site 1	0.6 + 0.2	0.2 + 0.3	1.2 + 0.5
Site 2	1.0 + 0.3	1.6 + 0.4	0.8 + 0.3
Site 3	3.2 + 0.7	5.0 + 1.2	2.2 + 0.6

transformed), but differences among the sites were detected ($F_{(2,4)} = 8.2$, $P < 0.05$). The density of females was consistently higher at Site 3 than at the other two sites (Table 2).

Experimental evaluation of the causes of patch location

Methods

Several recurrent patterns emerged over the three years the permanent quadrats were followed. Approximately the same areas of forest were heavily grazed by *Odax* in spring of each year, and these clearances were coincident with *Ecklonia* recruitment each year. A series of experiments, as outlined below, was done to test hypotheses derived from these observations.

Of the many processes that may account for these patterns, two experimentally tractable hypotheses were tested. The first postulated that these areas were, in themselves, important to the fish. Under this model the removal of plants was a side effect of the aggregation of fish at those places. An alternative hypothesis centred on the *Ecklonia* plants found in those areas. The great majority of plants in patches recruited after the previous episode of intense feeding and so were approximately one year old. Plants in surrounding areas of forest were not solely of this age group and may have been up to 4-5 years old (Andrew 1988). It was therefore reasoned that, for whatever reason, the intensity of herbivory was predicated on the age of the plants and older plants were avoided.

Core design. The central core of the experiments designed to test hypotheses based on these (non-mutually exclusive) models was an orthogonal array of two factors (Fig. 6A). The first factor, called Position, had two levels; Patch-areas of *Ecklonia* forest cleared by *Odax* the previous year and Forest-areas that had not been cleared. The second factor was called Treatment and was based on manipulations of either the density or age of plants (see below). Treatment had two levels: Regrowth and Clearance (Fig. 6A).

Regrowth plots were created in November 1986 either by clearing 4 m² areas not cleared by *Odax*, thereby simulating the effects of *Odax* outside areas normally cleared, or by establishing plots in areas grazed by the fish. *Ecklonia* then recruited into these areas and a canopy was permitted to re-establish itself. This generated, in July 1987, plots of one year old *Ecklonia* both outside and within areas normally grazed by *Odax* (Fig. 6A). The second level, Clearance, consisted of plots from which *Ecklonia* was removed in November 1986, and maintained free of *Ecklonia*. The core orthogonal component of the experiment was therefore made up of the four possible combinations of these treatments (Fig. 6A). Each treatment was repeated three times. Variations on this basic plan were used to test hypotheses as follows.

Damage to *Ecklonia*. To test the hypothesis that herbivory of *Ecklonia* by *Odax* was dependent on the position of plants, damage

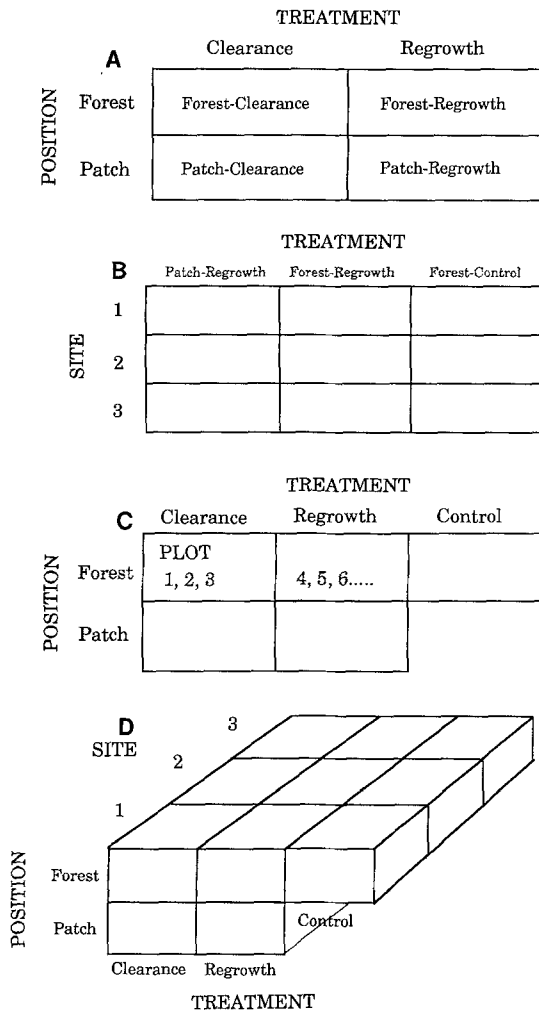


Fig. 6A–D. Experimental designs for testing different hypotheses about the location of feeding by *Odax*. **A** Core orthogonal array of Position (with levels Forest and Patch) and Treatment (with levels Clearance and Regrowth). **B** Orthogonal comparison of damage to *Ecklonia* in Patch-Regrowth, Forest-Regrowth, and Forest-Control treatments at three sites. **C** Comparison of *Odax* feeding intensity (time spent in plots) in all five treatments at site 1. **D** Design used to examine the effects of naturally and experimentally cleared quadrats on recruitment of *Ecklonia*

to individual plants in Patch-Regrowth plots was compared to that in Forest-Regrowth plots (Fig. 6B). In addition, at each site, three control quadrats were added to the design. These consisted of unmanipulated plots within forested areas (Forest-Control, Fig. 6B). In these plots plants were not only outside the areas normally cleared by *Odax*, but were comprised of mixed-age plants. Comparisons among the above treatments separated the effects of age and position of plants. By definition, the clearance treatments were excluded from consideration. This comparison was repeated at three sites. The design was, therefore, orthogonal with two factors; Treatment (fixed) with three levels and Site (random) with three levels (Fig. 6B). The same sites used for the descriptive work were used for the experiments. These sites were at least 50 m apart and had sufficient areas of *Odax* damage in November 1986 to support the experimental plots. Each treatment was repeated at each site in three 4 m² plots. The combined density of stubs and the numbers of plants per plot with recognizable bites by *Odax* was used as an estimator of damage.

Behaviour of *Odax*. *Odax* were observed to be largely restricted to *Ecklonia* forest habitat in preference to areas of reef covered

by crustose or turfing coralline algae. The hypothesis that *Ecklonia* was required in an area in order for it to be occupied by *Odax* was tested by comparing the rates of occupancy of *Odax* in cleared and regrowth plots in and outside traditional areas. The design therefore used the core orthogonal comparisons described above (Fig. 6A), with two additional comparisons (Fig. 6C). The Forest-Control treatment was considered as a non-orthogonal control and compared to treatments in the orthogonal component of the design (see Winer 1971 for a discussion of these designs). The Treatment \times Position interaction tested the hypothesis that the relationship between the presence of *Ecklonia* and the abundance of *Odax* was dependent on the history of the *Ecklonia* forest at that place. The second addition to the core design was the factor Plot which was nested within the Treatment \times Position interaction term.

The behaviour of individual *Odax* within the experimental plots was described in September 1987. Each of the three plots were observed three times, each for 15 min, and the times all individual *Odax* spent within each plot was recorded.

Recruitment of *Ecklonia*. One of the more intriguing aspects of the herbivory of *Ecklonia* by *Odax* was its timing. The effect of the massive clearance of *Ecklonia* was, at least in the short term, ameliorated by subsequent recruitment of *Ecklonia* into the freshly created gaps in the canopy (see Fig. 2B). The complete version of the design outlined above was used to test hypotheses concerning the ability of *Ecklonia* to re-establish itself in areas with different histories of disturbance (Fig. 6D). The combined density of juvenile and recruit plants was counted in all combinations of Regrowth and Clearance treatments and in the Forest-Controls. This array was repeated at all three sites. The model was therefore a three factor mixed model with two non-orthogonal comparisons (Fig. 6D). The factors Treatment, Position and Site were orthogonal. Within each site the forest control was compared to the mean of all other treatments within the site and the constancy, or otherwise, of that relationship was tested among sites. The combined density of juveniles and recruits was estimated in November 1987. This design was also used to compare the densities of other species of algae, *Sargassum* spp., *Zonaria* spp., *Dellisea pulchra*, and the herbivorous gastropods *Australium tentiforme* and *Turbo torquata* among experimental plots.

Experimental results

Damage to *Ecklonia*. Treatment and Site significantly interacted in influencing the amount of damage done to individual *Ecklonia* plants by *Odax* (Table 3, Fig. 7). At all sites, forest grazed by *Odax* in 1986 and allowed to regrow suffered significantly more (Table 3, Ryan's test) damage in 1987 than either of those treatments not cleared by *Odax* in the previous year (Fig. 7). Only at Site 2 was there significantly more damage sustained between plots that had been cleared and allowed to regrow (Forest-Regrowth) and the Forest-Control plots (Fig. 7, Table 3, Ryan's test). There were significant dif-

Table 3. Analysis of variance of damage to adult *Ecklonia* plants by *Odax* in experimental treatments containing *Ecklonia* in November 1987. Data $\log(x+1)$ transformed. See Fig. 6b for design

Source of variation	df for F	MS	F
Treatment	2, 4	1.96	11.35*
Site	2, 18	0.13	2.41 NS
T \times S	4, 18	0.17	3.28*
Residual		0.05	

* indicates $P < 0.05$

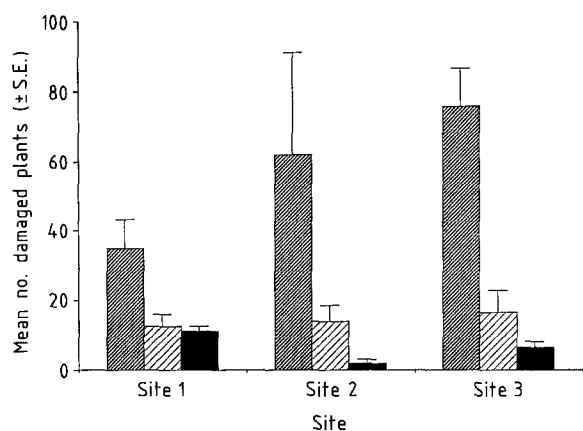


Fig. 7. Mean density (per 4 m² ± S.E., n=3) of damaged *Ecklonia* plants (stubs and plants with *Odax* bite marks) in Patch-Regrowth, Forest-Regrowth, and Forest-Control treatments at three sites

Table 4. Analysis of variance of A. Female, and B. Male *Odax* behaviour (mean time spent in experimental plots in September 1987). Data square root transformed prior to both analyses. See Fig. 6c for design

Source of Variation	df for F	A. Females		B. Males	
		MS	F	MS	F
Control vs Rest	1, 10	0.16	0.01 NS	2.14	0.56 NS
Treatment	1, 10	68.71	6.51 *	17.40	4.53 NS
Position	1, 10	80.90	5.53 *	1.50	0.39 NS
T × P	1, 10	34.72	2.80 NS	4.58	1.19 NS
Plot _(T × P)	10, 30	12.42	2.11 NS	3.84	1.77 NS
Residual		5.89		2.17	

* indicates $P < 0.05$

ferences among sites within each treatment only among the Forest-Control plots (Fig. 7, Ryan's tests). Within these treatments there was significantly less damage to *Ecklonia* at Site 2 than at either Site 1 and 3, which were not significantly different (Ryan's tests).

Behaviour of *Odax*. Females spent significantly more time in Regrowth plots than in Clearance plots, irrespective of whether those plots were in areas traditionally cleared by *Odax* (Table 4a, Fig. 8). 96% of the total time spent by females in experimental plots was concentrated in plots containing kelp (Fig. 8). It is notable that the two plots with the greatest foraging activity by females were patches cleared by *Odax* in 1986, in which *Ecklonia* was allowed to reestablish. Of 35 feeding bites observed in this experiment, 80% were from Patch-Regrowth plots and females accounted for 93% of those bites. This suggests that females were returning to traditional areas to forage, regardless of the age of the kelp stand. Very little activity was observed in one of the Patch-Regrowth plots; this patch was substantially cleared of *Ecklonia* when the observations were made (G.P. Jones pers. obs.). No significant differences in the activity of males between Regrowth and Clearance treatments were detected (Table 4b, Fig. 8). There were no significant differences

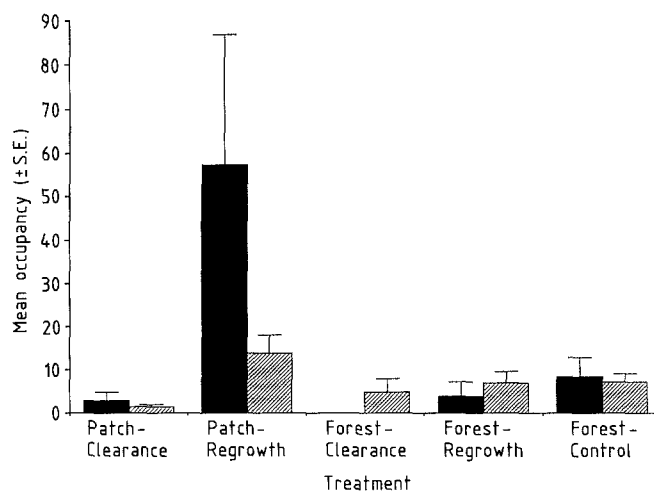


Fig. 8. Mean time spent (secs) by individual female and male *Odax* in the experimental treatments. Data pooled across plot, n=9

Table 5. Analysis of variance of recruitment by *Ecklonia* into experimental plots at three sites in November 1987, see Fig. 6d for design. Data square root transformed prior to analysis

Source of Variation	df for F	MS	F
Control vs Rest	1, 2	0.80	1.04 NS
Treatment	1, 2	59.96	3.33 NS
Position	1, 2	59.52	15.28 NS
Site	2, 30	22.98	26.60 **
Treatment × Position	1, 2	3.00	0.82 NS
Treatment × Site	2, 30	18.01	10.42 **
Position × Site	2, 30	3.90	2.25 NS
(Control vs Rest) × Site	2, 30	0.77	0.45 NS
Treat. × Position × Site	2, 30	3.65	2.11 NS
Residual		1.72	

** indicates $P < 0.01$

among plots within treatments in the time spent in them by either males or females, nor did the control plots significantly differ from the mean of the orthogonal treatments (Table 4).

Recruitment of *Ecklonia*. In October 1986, immediately after the manipulations were done, analysis revealed significant differences in the combined density of recruit and juvenile *Ecklonia*. There was in significant Treatment × Position × Site interaction term ($F_{(2,30)} = 3.93$, square root transformed, see Table 5 for analytical model used). This result indicates that at the start of the experiment there were no consistent differences among the factors, nor was there any consistent interaction among any subset of the three. The experimental results can therefore be interpreted without considering the starting conditions of the treatments.

The removal of the forest canopy in October 1986 and the maintenance of zero adult *Ecklonia* density within experimental plots caused large differences in the combined density of recruit and juvenile *Ecklonia* in the treatments in November (1987 (Fig. 9). The magnitude of difference between plots in which a canopy had been al-

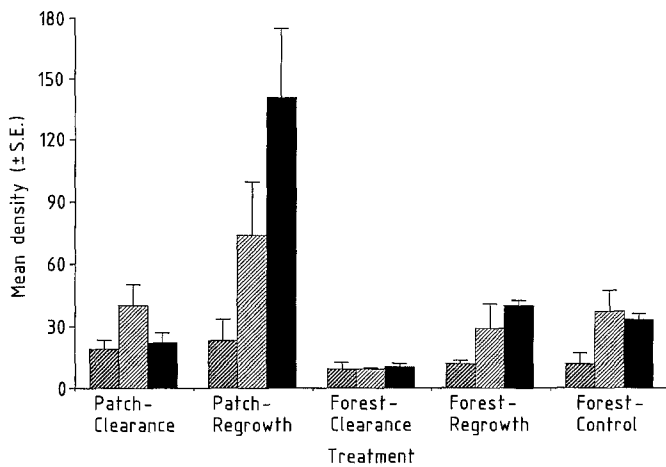


Fig. 9. Mean combined density (\pm SE, $n=3$) of *Ecklonia* recruits and juveniles in experimental plots in November 1987. ▨ Site 1; ▩ Site 2; ■ Site 3

lowed to re-establish differed among sites, as evidenced by a significant Treatment \times Site interaction term (Table 5). The density of recruits and juveniles in the Regrowth treatments (pooled across Position) was significantly greater than in the Clearance treatments at Sites 2 and 3 but not at Site 1 (Fig. 9, Ryan's test). The greatest density of sub-adult *Ecklonia* was found in the Regrowth treatment at Site 3 (92.3 ± 26.7 , $n=3$), which was significantly greater than at Site 2 which in turn was significantly greater than at Site 1 (Ryan's test). The combined density of recruit and juvenile *Ecklonia* in Clearance plots (pooled across Position) did not significantly differ among sites (Fig. 9, Ryan's test).

The analysis did not reveal any significant difference between control plots and the mean of all other treatments within a site (Table 5, Fig. 9). Nor was there any evidence that the relationship between 'forest' controls and all other treatments within a site differed among sites (Table 5, Fig. 9).

There was no significant difference between 'patch' and 'forest' areas in the density of sub-adult *Ecklonia* (Table 5, Fig. 9). The statistical power of the test of this factor was, however, weak (df for F test = (1, 2)), suggesting that it would be prudent to consider the location of the forest in future studies. Position did not interact significantly with either Site or Treatment (Table 5).

Discussion

Herbivory by Odax and patch dynamics

Browsing herbivorous fishes are well presented in temperate fish faunas, but there has been insufficient evidence to judge whether or not either feeding activities affect the distribution and abundance of macroalgae (see reviews by Choat 1982; Dayton 1985; Jones 1988). In this study, *Odax cyanomelas* was shown to have a major local impact on the structure and dynamics of patches within stands of the kelp *Ecklonia radiata*. *Ecklonia* is the dominant kelp on shallow rocky reefs in temperate

Australasia. The impact of *O. cyanomelas* at Cape Banks is site- and time-specific. The canopy of *Ecklonia* was totally removed at the same places (1–100 m² patches) and times (July–October) each year. The timing of this perturbation was coincident with the recruitment season of *Ecklonia*, and areas of forest decimated by fish were colonized by recruits shortly afterwards. Herbivory by these fish therefore generated dynamic patches consisting of a single age-class of plants. This contrasts with neighbouring areas, in which perennial, mixed-age, stands of *Ecklonia* exhibited more gradual changes in abundance.

The feeding activity of herbivorous fishes is frequently patchy in space and time (e.g. Choat and Bellwood 1985; Lewis 1986). The location and timing of herbivory by *Odax* appears to be associated with seasonal changes in behaviour related to spawning. Feeding by female *Odax* appears to be concentrated in traditional patches during the spawning months. Patches appear in areas in which females congregate prior to entering the territories of males and spawning near the deeper edge of kelp stands.

The experimental clearances did not favour an alternative hypothesis, that *Odax* are attracted to patches of one year old plants, rather than to traditional areas. The creation of new patches of young plants in the kelp forest adjacent to normal *Odax* clearances did not lead to any significant change in feeding patterns of *Odax*. These quadrats were well within the normal range of female movements, so there is no reason to indicate that they did not come into contact with these younger-aged stands.

Although preference for yearling plants might not be important, a preference for particular parts of *Ecklonia* plants did appear to accelerate patch formation. Bites by females were most often taken from the meristem and primary laminae. Loss of kelp and the formation of patches may be largely due to decapitation by *Odax*, rather than the total consumption of kelp plants. Even in those cases where the meristematic tissue was not completely removed, loss of tissue in this region considerably weakened the plants, making them more prone to storm damage.

The interpretation of changes in species abundance in the permanent quadrats requires some caution. The locations of the quadrats were fixed in October 1985, in areas that had either been cleared by *Odax*, or in surrounding areas that had an intact canopy of *Ecklonia*. In the two subsequent years not all quadrats in areas originally cleared were again and, conversely, some quadrats untouched in 1985 were at least partially cleared in later years. The former was more prevalent than the latter (N.L. Andrew pers. obs.). The effect of this spatial variability is to blur any differences between the two 'positions', and makes any comparisons between the two more conservative. This at least partially accounts for the lack of significant differences in the abundance of recruit and juvenile *Ecklonia* in these quadrats in subsequent years. Our perception was that the damage caused by *Odax* in the years we observed it was similar in areal extent and intensity but varied slightly in its timing and exact location.

With these constraints in interpretation in mind, there were interesting shifts in the combined abundance of *Zonaria* spp. and *Dellisea pulchra* in both 'patch' and 'forest' quadrats. In the latter part of 1985, and throughout most of 1986 there were considerably more of these turfing species in the 'patch' quadrats than in the 'forest' quadrats. These differences became less apparent in 1987 and 1988, at least partially due to an increase in the density of *Zonaria/Dellisea* in 'forest' quadrats. This increase coincided with a decrease in the density of adult *Ecklonia* in these quadrats, suggesting that there had been a slow shift in community structure toward an assemblage dominated by turfing algae. The cause of the decline in density of adult *Ecklonia* in these quadrats remains unclear but the relatively monotonic nature of the decline argues against an episodic phenomenon such as storm damage. The lack of any consistent difference in the the abundance of molluscan herbivores suggests that they play relatively little role in influencing this shift in habitat structure. In New South Wales turbinids and trochids have relatively little influence in shifts between the Bartens habitat and habitats dominated by foliose and turfing algae (Fletcher 1987). There is no experimental information on the effect of molluscs on the abundance of algae outside the Barrens habitat. It is conceivable that they may have a greater effect in *Ecklonia* forests as the abundance of recruits of foliose algae are likely to be far greater.

The importance of the timing of disturbance, algal life-histories and interactions among algae

The timing of disturbance to normal communities has been shown to be of great significance in determining subsequent community events (e.g. Dayton 1973; Paine 1979; Paine and Levin 1981; Dayton et al. 1984; Reed and Foster 1984; Sousa 1985; Kennelly 1987b). The availability of propagules will have a great impact on the composition of the colonizing assemblage, both in time (see above references), and in space. This is especially true for species with limited dispersal ability, such as many species of large brown algae (Dayton 1973; Paine 1979; Deysher and Norton 1982; Schiel 1985; Johnson and Mann 1988; Reed et al. 1988).

For a number of these species, the reproductive season coincides with the time of year when suitable space is most likely to become available, either through the removal of adult sporophytes or via the removal of space competitors (e.g. *Postelsia palmaeformis* (Dayton 1973; Paine 1979), *Macrocystis pyrifera* and *Pterogophora californica* (Cowen et al. 1982; Dayton and Tegner 1984; Ebeling et al. 1985; Reed et al. 1988). In the present study the intense herbivory of *Odax* was relatively predictable in both space and time and coincided with the recruitment season of *Ecklonia*. The effect of this intense herbivory was therefore similar to the effects of physical disturbance described above in that it has the potential to enhance the local persistence of *Ecklonia* through enhance recruitment and replacement of existing plants.

Had the *Ecklonia* been removed at any other time of the year (or if recruitment failed) then the canopy

would have been lost and replaced with a mixed assemblage of turfing aglae, principally articulated coralline algae and dictyotalean species (Kennelly 1987a, b). This latter community state has been shown to be relatively resistant to reinvasion by *Ecklonia* (Fletcher 1987; Kennelly 1987a, present study). The loss of *Ecklonia* forest from areas of reef, and consequent changes in the composition of assemblages of algae would have caused changes in the local distribution patterns of several species, particularly the benthic feeding fish *Cheilodactylus fuscus* (Andrew and Jones unpubl. data). For many species of fish in temperate regions, local abundance patterns reflect the disposition of habitats on the reef (e.g. Jones 1984; Choat and Ayling 1987; Bodkin 1988; Carr 1989).

The sequence of events in the recolonization of cleared patches is not known. Specifically, it is not known whether the sporophytes that 'appear' in cleared areas are produced by gametophytes present on the substratum before or after the canopy was removed. If the canopy-forming plants released spores prior to their removal then grazing by *Odax* may actually increase the short-term survivorship of these offspring through the provision of space suitable for the development of adult plants. Alternatively, fertile plants drifting over the reef may increase the survivorship of offspring through the colonization of reef previously 'unavailable' to those individuals. The colonization of new areas of reef by this method has been hypothesised by Dayton et al. (1984; but see Reed et al. 1988). The possibility that recruitment may be enhanced by either of these alternatives should be considered in discussions of the chemical defenses on these plants (see below). The possibility that *Ecklonia* may exhibit totally different life-history and reproductive characteristics in herbivore-damaged patches vs. forested areas should also be considered.

Herbivory by Odax and chemical defense in Ecklonia

There have been many demonstrations of the deterrent effect of secondary metabolites on the consumption of algae by a wide range of herbivores (e.g. Geiselman and McConnell 1981; Steinberg 1984, 1986; Johnson and Mann 1986; Targett et al. 1986; see Hay and Fenical 1988 for review). Analysis of the concentration of polyphenolic compounds in different parts of *Ecklonia* plants (Table 6) suggest that the intercalary meristem and primary lamina of adult plants are among the least defended parts of the plant. This pattern is interesting be-

Table 6. Levels of polyphenolics in different parts of adult *Ecklonia* plants at Cape Banks as measured in August 1988. Concentrations of polyphenolics determined by the Folis-Dennis assay (see Ragan and Jensen (1977) for methods). Data presented as mean +/- SE, n = 5

Stipe	Meristem	Primary laminae	Secondary laminae
2.14 +/- 0.17	2.51 +/- 0.50	3.94 +/- 0.94	8.24 +/- 0.44

cause the viability of an individual *Ecklonia* plant is dependent upon the integrity of the intercalary meristem. Its position at the top of the stipe means that it is readily available to a highly mobile herbivore like *Odax*. The patterns of herbivory observed in this study suggest that the disposition of polyphenolics in *Ecklonia* is not an effective defense against herbivory by *Odax*. Although *Odax* may be deterred by high levels of polyphenolics, the low level of polyphenolics in the primary meristem means that herbivory by *Odax* may be fatal. The disposition of polyphenolics in *Ecklonia* is in contrast to that of *Laminaria longicuris* in which the intercalary meristem is the most defended part of the plant (Johnson and Mann 1986). It was concluded by Johnson and Mann (1986) that this concentration of polyphenolics was crucial to the viability of the plant.

Of course *Odax* is only one of a number of herbivores known to consume *Ecklonia*: it is exposed to the very different preferences, mobilities, and habitat requirements of a diverse range of herbivores. If the allocation of chemical defenses in an alga is an evolutionary response to herbivory then the selective effect of all these herbivores must be considered. The consequences of being attacked by the sea urchin, amphipod, or an herbivorous fish may be quite different.

Several authors have noted that differing physiologies and modes of feeding among herbivores will decrease the effectiveness of any single defensive characteristic (e.g. Hay 1981, 1984; Gaines 1985; Hay et al. 1987). Taken a face value, the information presented in this paper suggested that the allocation of polyphenolics in *Ecklonia* is not an effective defense against herbivory by *Odax*. The correlative nature of this information means, of course that these results cannot be considered a test of hypotheses derived from a model based on the chemical defense of *Ecklonia* against attack by herbivores. There remains the possibility that herbivory by *Odax*, because of its timing, actually increases the survivorship of recruits by removing the canopy of adult plants.

Generality of *Odax* effect

We have demonstrated that herbivory by *Odax cyanomelas* has an intense effect on some kelp forests at one geographical location on the central coast of New South Wales. How important is grazing by this species in a more general sense, to the ecology of *Ecklonia* forests in temperate Australia? The relative importance of this interaction depends not only on its widespread occurrence, but also on other agents of change in kelp forests, such as available recruitment, physical disturbance, grazing by other herbivores, and plant-plant interactions.

Of these processes, grazing by the sea urchin *Centrostephanus rodgersii* has been shown to maintain areas free of all foliose algae, including *Ecklonia* (Fletcher 1987; Andrew and Underwood 1989). In contrast to the action of *Odax*, the effects of grazing by *Centrostephanus* are not only intense but also continuous. The results of this study suggest that *Odax* are almost totally re-

stricted to areas of dense *Ecklonia* forest, whereas *Centrostephanus* are principally found in areas of Barrens habitat (Fletcher 1987; Andrew and Underwood 1989). There is little spatial overlap between the two species in terms of the micro-habitats used, therefore the potential for interaction between the two species is relatively low. This apparent lack of interaction is brought about by an extremely asymmetrical relationship. Grazing by *Centrostephanus* has very great effects on the abundance and local distribution of *Ecklonia*; the effect of *Centrostephanus* on *Odax* is therefore very great. The reverse does not appear to be the case.

The degree to which herbivory by *Odax* contributes to the long-term patterns in the abundance of *Ecklonia* is uncertain. If it were not for the fact that *Ecklonia* were able to immediately recolonize denuded areas of reef, we would expect this herbivory to lead to a totally different habitat structure. Such a shift in the species composition and abundance of algae would also prompt changes in the abundance patterns of fish and invertebrate herbivores. If the intense herbivory by *Odax* observed in this study did not coincide with recruitment by *Ecklonia* then the shallow subtidal communities of New South Wales would be considerably more patchy, both in space and time.

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References

- Andrew NL (1988) Population dynamics and herbivory in the common sea urchin *Centrostephanus rodgersii*, Ph.D. Thesis, University of Sydney, p 148
- Andrew NL, Choat JH (1982) The influence of predation and conspecific adults on the survivorship of juvenile *Evechinus chloroticus* (Echinoidea: Echinometridae). *Oecologia* 54:80-87
- Andrew NL, Underwood AJ (1989) Patterns of abundance in the sea urchin *Centrostephanus rodgersii* on the central coast of New South Wales, Australia. *J Exp Mar Biol Ecol* 131:61-80
- Atkinson WD, Shorrocks B (1981) Competition for a divided and ephemeral resource: a simulation model. *J Anim Ecol* 50:461-471
- Auerbach M, Shmida A (1987) Spatial scale and the determinants of plant species richness. *TREE* 2:238-242
- Bodkin JL (1988) Effects of kelp forest removal on associated fish assemblages in central California. *J Exp Mar Biol Ecol* 117:227-238
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. *Ecol Monogr* 56:345-363
- Carr MH (1989) Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *J Exp Mar Biol Ecol* 126:59-76
- Chapman ARO (1981) Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, eastern Canada. *Mar Biol* 62:307-311

- Choat JH (1982) Fish feeding and the structure of benthic communities in temperate waters. *Ann Rev Ecol Syst* 13:423–449
- Choat JH, Ayling AM (1987) The relationship between habitat structure and fish faunas on New Zealand reefs. *J Exp Mar Biol Ecol* 110:257–284
- Choat JH, Bellwood DR (1985) Interactions among herbivorous fishes on a coral reef: influence of spatial variation. *Mar Biol* 89:221–234
- Connell JH, Keough MJ (1985) Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: Pickett STA, White PS (eds) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, pp 125–151
- Cowen RK, Agegian CR, Foster MS (1982) The maintenance of community structure in a central California giant kelp forest. *J Exp Mar Biol Ecol* 64:189–201
- Day RW, Quinn GP (1989) Comparisons of means after an analysis of variance in ecology. *Ecol Monogr* 59:433–463
- Dayton PK (1973) Dispersion, dispersal and persistence of the annual intertidal alga *Postelsia palmaeformis* Ruprecht. *Ecology* 54:433–438
- Dayton PK (1985) Ecology of kelp communities. *Ann Rev Ecol Syst* 16:215–245
- Dayton PK, Currie V, Gerrodette T, Keller BD, Rosenthal R, Ven Tresca D (1984) Patch dynamics and stability of some California kelp communities. *Ecol Monogr* 54:253–289
- Dayton PK, Tegner MJ (1984) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Price PW, Slobodchikoff CN, Gaud WS (eds). *A new ecology: novel approaches to interactive systems*. John Wiley & Sons, New York, pp 457–481
- Deysler L, Norton TA (1982) Dispersal and colonization in *Sargassum muticum*. *J Exp Mar Biol Ecol* 56:179–195
- Ebeling AW, Laur DR, Rowley RJ (1985) Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Mar Biol* 84:287–294
- Fletcher WJ (1987) Interactions among subtidal Australian sea urchins, gastropods, and algae: effects of experimental removals. *Ecol Monogr* 57:89–109
- Gaines SD (1985) Herbivory and between-habitat diversity: the differential effectiveness of defenses in a marine plant. *Ecology* 66:43–485
- Geiselman JA, McConnell OJ (1981) Polyphenols in the brown algae *Fucus vesiculosus* and *Ascophyllum nodosum*: chemical defense against the herbivorous snail *Littorina littorea*. *J Chem Ecol* 7:1115–1133
- Gomon MF, Paxton JR (1985) A revision of the Odacidae, a temperate Australian-New Zealand labroid fish family. *Indo-Pacific Fishes* 8:1–57
- Harris LG, Ebeling AW, Laur DR, Rowley RJ (1984) Community recovery after storm damage: a case of facilitation in primary succession. *Science* 224:1336–1338
- Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* 66:1160–1169
- Hay ME (1981) Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *Am Nat* 118:520–540
- Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65:446–454
- Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. *Ann Rev Ecol Syst* 19:111–145
- Hay ME, Fenical W, Gustafson K (1987) Chemical defense against diverse coral reef herbivores. *Ecology* 68:1581–1591
- Heck KL Jr, Orth RJ (1980) Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy VS (ed) *Estuarine perspectives*. Academic Press, New York, pp 449–464
- Holbrook SJ, Schmitt RJ (1988) Effects of predation risk and foraging behaviour: mechanisms altering patch choice. *J Exp Mar Biol Ecol* 121:151–163
- Horn MH (1983) Optimal diets in complex environments: feeding strategies of two herbivorous fishes from a temperate intertidal zone. *Oecologia* 58:345–350
- Johnson CR, Mann KH (1986) The importance of plant defence abilities to the structure of subtidal seaweed communities: the kelp *Laminaria longicuris* de la Pylaie survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. *J Exp Mar Biol Ecol* 97:231–267
- Johnson CR, Mann KH (1988) Diversity, patterns of adaptation and stability of Nova Scotian kelp beds. *Ecol Monogr* 58:129–154
- Jones GP (1984) Population ecology of a temperate reef fish *Pseudolabrus celidotus* Bloch and Schneider (Pisces: Lartidae). I. Factors affecting recruitment. *J Exp Mar Biol Ecol* 75:257–276
- Jones GP (1988) Ecology of rocky reef fishes of north-eastern New Zealand: a review. *NZ J Mar Freshwat Res* 22:445–462
- Kennelly SJ (1987a) Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. *J Exp Mar Biol Ecol* 112:49–60
- Kennelly SJ (1987b) Physical disturbances in an Australian kelp community. I. Temporal effects. *Mar Ecol Prog Ser* 40:145–153
- Kennelly SJ (1987c) Physical disturbances in an Australian kelp community. II. Effects on understory species due to differences in kelp cover. *Mar Ecol Prog Ser* 40:155–165
- Keough MJ (1984) Effects of patch size on the abundance of sessile marine invertebrates. *Ecology* 65:423–437
- Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol Monogr* 56:183–200
- Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Ann Rev Ecol Syst* 12:405–437
- Morris DW (1987) Ecological scale and habitat use. *Ecology* 68:362–369
- Paine RT (1979) Disaster, catastrophe and local persistence of the sea palm *Postelsia palmaeformis*. *Science* 205:685–687
- Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol Monogr* 51:145–178
- Peterson CH (1982) Clam predation by whelkes (*Busycon* spp.): Experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar Biol* 66:159–170
- Pickett STA, White PS (1985) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York
- Ragan MA, Jensen A (1977) Quantitative studies on brown algal polyphenols. I. Estimation of absolute polyphenol content of *Ascophyllum nodosum* (L.) and *Fucus vesiculosus* (L.). *J Exp Mar Biol Ecol* 34:245–258
- Reed DC, Foster MS (1984) The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65:937–948
- Reed DC, Laur DR, Ebeling AW (1988) Variation in algal recruitment: the importance of episodic events. *Ecology* 69:321–335
- Ricklefs RE (1977) Environmental heterogeneity and plant-species diversity: a hypothesis. *Am Nat* 111:376–381
- Sammarco PW (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. *Mar Ecol Prog Ser* 13:1–14
- Schiel DR (1985) Growth, survival and reproduction of two species of marine algae at different densities in natural stands. *J Ecol* 73:199–217
- Schiel DR (1988) Algal interactions on shallow subtidal reefs in northern New Zealand: a review. *NZ J Mar Freshwat Res* 22:481–489
- Schiel DR, Foster MS (1986) The structure of subtidal algal stands in temperate waters. *Oceanogr Mar Biol Annu Rev* 24:265–307
- Scott FJ, Russ GR (1987) Effects of grazing on species composition of the elipthic algal community on coral reefs of the central Great Barrier Reef. *Mar Ecol Prog Ser* 39:293–304
- Sousa WP (1984) The role of disturbance in natural communities. *Ann Rev Ecol Syst* 15:353–391
- Sousa WP (1985) Disturbance and patch dynamics on rocky inter-

- tidal shores. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp 101–124
- Steinberg PD (1984) Algal chemical defense against herbivores: Allocation of phenolic compounds in the kelp *Alaria marginata*. *Science* 223:405–407
- Steinberg PD (1986) Chemical defenses and the susceptibility of tropical marine brown algae to herbivores. *Oecologia* 69:628–630
- Targett NM, Targett TE, Vrolijk NH, Ogden JC (1986) Effect of macrophyte secondary metabolites on feeding preferences of the herbivorous parrotfish *Sparisoma radians*. *Mar Biol* 92:141–148
- Tonn WM, Magnuson JJ (1982) Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63:1149–1166
- Wiens JA (1985) Vertebrate responses to environmental patchiness in arid and semi-arid ecosystems. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp 169–193
- Wiens JA, Rotenberry JT (1981) Habitat associations and community structure of birds in shrubsteppe environments. *Ecol Monogr* 51:21–41
- Winer BJ (1971) *Statistical principles in experimental design*. McGraw-Hill, Kogakusha, Tokyo