

The Effects of Altering Seagrass Canopy Height on Small, Motile Invertebrates of Shallow Mediterranean Embayments

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With 5 figures and 7 tables

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Abstract. The height of seagrass canopy was manipulated in experimental plots in meadows of the fine-leaves seagrass *Cymodocea nodosa* at two sites in the Mediterranean Sea, la Lagune du Brusuc, Iles des Embiez near Toulon, and l'Etang de Diana on Corsica. Epifauna (small motile invertebrates associated with the seagrass canopy or sediment surface), was collected at night at both sites, and during the day at Diana only, from three treatments: full seagrass canopy, reduced canopy, and canopy removed entirely. Although epifaunal assemblages from the two sites were different, treatment modification had the same effect at both sites when analysed using multivariate ordinations. Abundance and biomass of total epifauna and of key taxa were all reduced in line with decreasing seagrass cover at both sites at night. The effects of treatment modification on epifauna during the day showed the same trend but were of greater magnitude, both for assemblages and for total abundance and biomass. At both sites and at both times, the fauna of plots from which seagrass had been cut tended to be dominated by animals of higher biomass than the fauna of plots with full canopy. Epifauna form the major dietary component of small fish inhabiting shallow, sheltered embayments. These results are therefore consistent with a model in which reduced abundance of fish associated with reduced seagrass canopy is explained by a reduction in food availability.

Problem

The abundance of small, motile invertebrates associated with seagrass is typically greater than that associated with adjacent unvegetated patches (ORTH, 1977; STONER, 1980; ORTH *et al.*, 1984) though exceptions have been reported and the importance of the canopy may be overridden by other factors (YOUNG & YOUNG, 1982; BELL & WESTOBY, 1986a; BELL *et al.*, 1987; SOGARD *et al.*, 1987; HOLMQUIST *et al.*, 1989; SOGARD, 1989). This difference is more obvious for epifauna (animals associated with the leaf and sediment surfaces) than infauna (animals buried within the sediment) (HOWARD *et al.*, 1989). At certain sites, including some in the

Mediterranean, much of the fauna has been identified to specific level and the nature of the association is well documented; it varies in detail between sites, depths, and with structure of the vegetation (LEDOYER, 1968; GAMBÌ *et al.*, 1992; GIANGRANDE & GAMBÌ, 1986; MAZZELLA *et al.*, 1992; LANERA & GAMBÌ, 1993).

Although some influence is attributed to structural habitat complexity (number of available niches), the two most commonly invoked explanations for the greater abundance of epifauna associated with vegetated habitats are that seagrass provides protection from predation or a greater abundance of food. The role of seagrass in providing protection from predators has received most attention in recent times (HECK & ORTH, 1980, and see review by HOWARD *et al.*, 1989). The work of BELL & WESTOBY (1986b) demonstrated that, for the macrofauna they studied, lower abundance in patches with less seagrass cover was not due simply to predators eating the target species. Macrofauna were rarer in patches with less cover regardless of the presence or absence of predators. BELL & WESTOBY (1986c) suggested that macrofauna select patches with more cover (and pointed out that predation may have been the ultimate selective agent for this behaviour). Although less experimental work has been done on smaller epifaunal invertebrates (HOWARD *et al.*, 1989), harpacticoid copepods are known to colonise artificial seagrass placed near natural seagrass beds (BELL & HICKS, 1991).

Abundances of small fish are also greater in seagrass than in adjacent unvegetated areas (ORTH & HECK, 1980; WEINSTEIN & BROOKS, 1983; OLNEY & BOEHLERT, 1988; BELL & POLLARD, 1989; CONNOLLY, 1994a), and seagrass meadows are thought to provide nursery areas for juveniles of many commercially important species (POLLARD, 1984). For this and other reasons there is concern about the worldwide loss of seagrass (SHEPHERD *et al.*, 1989), which has been associated with declining fish catches (*e.g.*, BELL & POLLARD, 1989). To enable wise management decisions, the reasons for the association between fish and seagrass need to be understood. The association is clearly complex and variable, as is the dynamics of the epifauna, depending on the structural characteristics of the vegetation (*e.g.*, STONER, 1980; ORTH *et al.*, 1984; HALL & BELL, 1988; EDGAR, 1990a).

Small fish associated with seagrasses are predominantly carnivorous. Although there are variations in detail, the general pattern is that epifaunal invertebrates form the major part of their diet (ADAMS, 1976; KLUMPP *et al.*, 1989), and in particular this is so in the Mediterranean (CASABIANCA & KIERNER, 1969; BELL & HARMELIN-VIVIEN, 1983; KHOURY, 1984) and the Black Sea (DUKA, 1978). This study is part of a series of experiments aiming to elucidate the relationship between seagrass loss, fish abundances, and epifaunal assemblages (CONNOLLY, 1994a, b, c, d, 1995a); the epifauna was sampled with this in mind.

This paper presents the results of field manipulations at two Mediterranean locations to test the hypothesis that alterations of seagrass canopy height (and hence its surface area) alters epifaunal abundance and community structure.

Material and Methods

1. Experimental design and sampling

Experiments were done in shallow, sheltered embayments in la Lagune du Brusac near the shore of l'Ile des Embiez (near Toulon, France) and l'Etang de Diana on Corsica (Fig.1), where the dominant

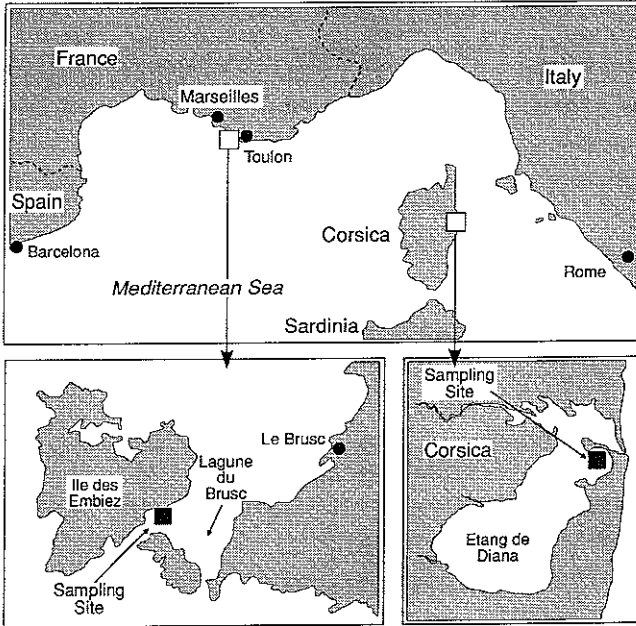


Fig. 1. Location of sites.

vegetation is the fine-leaved seagrass *Cymodocea nodosa*. These sites are referred to below as Embiez and Diana, respectively. The small motile invertebrates associated with the seagrass canopy and sediment surface (epifauna) were collected from the following three treatments marked as 1 m × 1 m plots:

- (1) seagrass uncut (control = C),
- (2) seagrass canopy cut to one third of original height (partly cut = P), and
- (3) seagrass canopy removed entirely (removed = R).

Seagrass was cut using hand shears and was shaken vigorously in the water before being removed to minimise the amount of epifauna carried away from the plot. The disturbance associated with cutting was simulated in control plots by spending an equivalent time mimicking cutting.

At each location, six plots were assigned to each of the treatments in a randomized block design. That is, one replicate of each treatment was assigned at random to six areas (blocks) strung along a 300 m stretch of coast at Diana and placed in a 0.25 ha area adjacent to the coast at Embiez. All plots were between 10 and 30 m from the shore at both locations. At Diana an additional four replicates of each treatment were set up for collection of epifauna during the day. All other sampling was done immediately after dusk. The blocked design guaranteed interspersion, which is important because of the potential patchiness of epifauna. All plots were in water between 30 and 70 cm deep. Both locations are characterised by relatively small tidal ranges (during the experiments the water height fluctuated 12 cm at Embiez and 2 cm at Diana), fine sediments, salinities approximating those of open seas (about $35 \text{ g} \cdot \text{l}^{-1}$) and warm summer water temperatures (approx. 25°C at time of night sampling).

Epifauna was collected by using a $150 \mu\text{m}$ mesh net with a $25 \times 25 \text{ cm}$ opening following the method of SERGEEV *et al.* (1988) in which the net is placed rapidly over the canopy onto the sediment before dragging shut the mouth of the net along the sediment surface. This method has been used previously in experiments in which a similar type of seagrass canopy (*Zostera*) was manipulated (CONNOLLY, 1995b). Samples were taken 2 days after the setting up of treatments, and the order in which plots were sampled was randomised. One sample was taken approximately in the centre of each plot. Animals were later separated into sieve size classes of 2 mm, 1 mm, $500 \mu\text{m}$, $250 \mu\text{m}$, and $125 \mu\text{m}$ before being identified to major taxa and counted. A smaller sieve size ($75 \mu\text{m}$) well below the mesh size of the collecting net was also used when sorting but this retained very few organisms, and although animals

retained on it have been included in analyses, their inclusion makes little practical difference to results. Numbers of very abundant taxa were counted from random subsamples with the aim of counting between 50 and 200 individuals of each taxon per sieve size in any sample. Abundances were determined for twenty-two taxa, 13 crustacean and 9 others (Table 1). Nematodes and foraminiferans were excluded from this study because they are typically not an important component in the diet of small fish inhabiting seagrass meadows (KLUMPP *et al.*, 1989; but see GEE, 1989, for an exception). Ash-free dry weights (AFDW) were calculated by converting abundances for each taxon for each sieve size using EDGAR'S (1990b) equation, $\log B = a + b \cdot \log S$ (where $B = \text{AFDW (mg)}$, $S = \text{sieve size (mm)}$ and a and b vary depending on broad taxonomic category).

The length and leaf area index (LAI, defined in BULTHOIS, 1990) of seagrass leaves in each plot were estimated prior to cutting and after epifauna collection. LAI was calculated for each plot by counting the number of leaves per 100 cm² quadrat and measuring the length and width of 10 leaves at three randomly selected places. All vegetation was *Cymodocea nodosa* except for occasional *Zostera noltii* plants at Diana.

2. Data analysis

Epifaunal assemblages (described both by abundance and biomass (AFDW) from the three treatments were compared using an analysis of similarities (ANOSIM), which is a non-parametric analogue to a multivariate analysis of variance (MANOVA) without the assumption of multivariate normality. ANOSIM has an additional advantage over MANOVA in being able to detect differences between groups without the assumption of similar variance within each group (CLARKE, 1993). ANOSIM compares ranked similarities between and within groups selected *a priori* (here the three treatments) using a randomisation test for significance. After a significant difference has been detected using this global ANOSIM test, the same technique is employed to test pairwise differences. Assemblages from the three 'collections' Embiez, Diana-Night and Diana-Day, were also compared using a two-way crossed ANOSIM with treatment as the second factor. This analysis determines whether assemblages differed amongst the collections after accounting for treatment differences. All ANOSIM tests involved 5000 simulations using the PRIMER package from Plymouth Marine Laboratory, UK.

The relationships amongst assemblages from each plot are graphically represented using non-metric multidimensional scaling (MDS), an ordination technique that uses the same matrix of ranked similarities as ANOSIM. MDS displays samples in low-(usually-two-) dimensional space while retaining as nearly as possible the similarity rankings between samples.

For comparisons of epifaunal assemblages, raw counts were transformed using $x^{0.25}$ to emphasise the

Table 1. List of taxa into which animals were grouped. Abbreviations shown are those used in Tables 3 and 6.

	Crustacea		non-Crustacea
	Caridea	Pol	Polychaeta
Mys	Mysidacea	Gas	Gastropoda
Amp	Amphipoda-Gammaroidea	Biv	Bivalvia
	Amphipoda-Caprelliidea		Ophiuroidea
Tan	Tanaidacea		Echinodermata, larvae
Iso	Isopoda	Ane	Actiniaria (Anemones)
	Cumacea		Chaetognatha
Har	Copepoda-Harpacticoida	Chi	Chironomidae, larvae
Por	Copepoda-Harpacticoida-Porcellidiidae		Ascidiacea, larvae
Cyc	Copepoda-Cyclopoida		
Cal	Copepoda-Calanoidea		
	Copepoda-nauplii (unidentified)		
	Ostracoda		

distribution of less common taxa in the analysis (CLARKE, 1993). The BRAY-CURTIS similarity coefficient was used throughout as a meaningful and robust measure of community structure (CLARKE, 1993).

Analysis of the similarity matrix used in MDS and ANOSIM has also been used to identify the taxa making the largest contribution to between-group differences (CLARKE, 1993).

The abundance and biomass of epifauna (all taxa combined as well as key taxa separately) from the three treatments were compared using analysis of variance (ANOVA) with TUKEY's HSD pairwise comparisons following significant ANOVA results. Differences between the three 'collections', Embiez, Diana-Night, and Diana-Day, in the above variables were compared to using a two-factor ANOVA with treatment as the second, fixed factor. All univariate analyses were performed on $\log_{10} x$ transformed data (or $\log_{10}(x+1)$ where zeros occurred) after checking that the transformation increased homoscedasticity (F_{\max} test). Significance levels are 0.05 throughout this paper.

Results

1. Canopy height and leaf area index

Leaf lengths and leaf area indices (LAIs) prior to cutting and at the time of epifauna collection are shown in Table 2.

2. Multivariate analyses

Two-dimensional ordination plots show strong grouping of plots from the three treatments both for abundance and biomass in all collections (Figs 2–4). Results of ANOSIM comparisons amongst assemblages separately for each collection are shown in Table 3. At Embiez, assemblages were significantly different for both

Table 2. Leaf lengths (mm) and Leaf Area Indices (m^2 leaf area per m^2 sediment surface area) prior to cutting and at time of epifauna collection. Numbers are means for each treatment, with standard errors in parentheses. C = control, P = partly cut, R = removed.

location, treatment	leaf lengths		leaf area index	
	prior to cutting	at time of collection	prior to cutting	at time of collection
EMBIEZ				
C	161 (8.7)	171 (8.8)	3.63 (0.31)	3.79 (0.38)
P	152 (9.9)	56 (2.3)	3.12 (0.47)	1.09 (0.09)
R	167 (8.6)	18 (2.0)	3.52 (0.08)	0.06 (0.01)
DIANA-NIGHT				
C	281 (26.3)	273 (22.2)	4.67 (0.95)	4.62 (0.89)
P	281 (28.0)	82 (6.9)	5.09 (1.04)	1.11 (0.17)
R	268 (25.7)	14 (1.9)	4.57 (0.93)	0.05 (0.01)
DIANA-DAY				
C	269 (25.3)	262 (27.2)	4.72 (0.90)	4.47 (0.75)
P	270 (17.7)	79 (7.1)	4.75 (0.62)	0.99 (0.16)
R	257 (24.0)	13 (2.1)	4.60 (0.61)	0.04 (0.01)

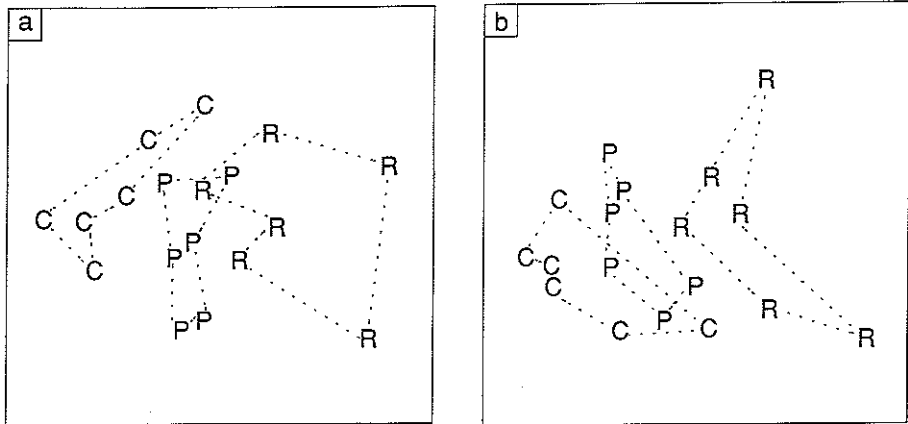


Fig. 2. Two-dimensional MDS ordination plots of epifaunal assemblages from Ile des Embiez based on a. abundance (stress = 0.146) and b. biomass (0.138) data. C = control; P = partly cut; R = removed.

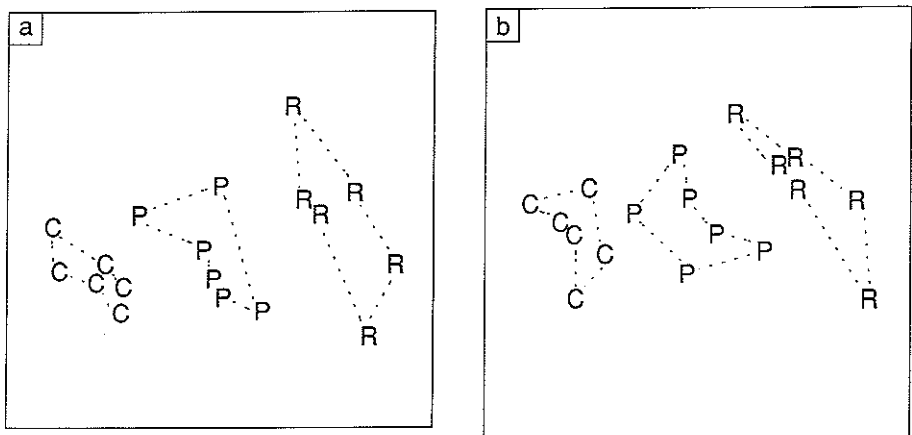


Fig. 3. Two-dimensional MDS ordination plots of epifaunal assemblages from Etang de Diana-Night based on a. abundance (stress = 0.068) and b. biomass (0.073) data. C = control; P = partly cut; R = removed.

abundance and biomass. Pairwise ANOSIM comparisons showed that abundances were significantly different amongst the three treatments, while biomass data for treatment R were different from treatments C and P. At Diana-Night, all treatments differed according to pairwise ANOSIM tests. At Diana-Day, pairwise ANOSIM comparisons were significant only between treatments C and R based on abundances. Results for the other comparisons had probabilities not much higher than the 0.05 critical level. Although no formal statistical power calculations are possible with this method, due to the low number of plots (four) from each treatment, a failure to detect differences does not mean that no difference exists. Based on

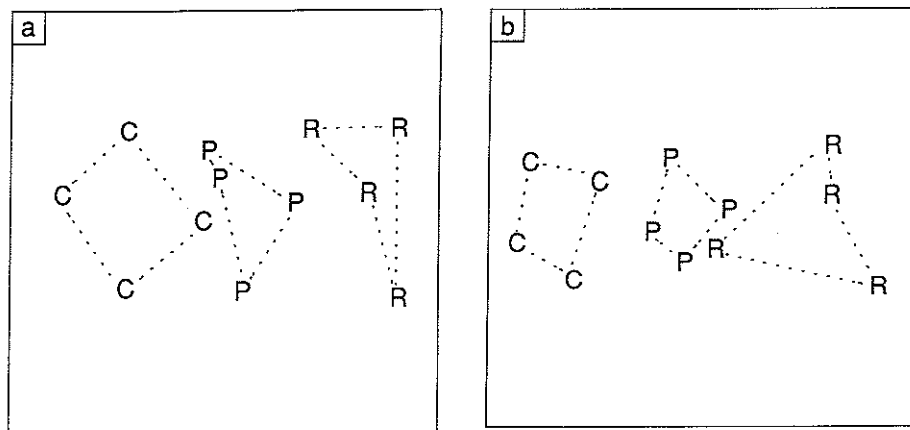


Fig. 4. Two-dimensional MDS ordination plots of epifaunal assemblages from Etang de Diana-Day based on a. abundance (stress = 0.073) and b. biomass (0.042) data. C = control; P = partly cut; R = removed.

biomass data, C was different from P and R, with these two treatments not shown to be different, although the above warning about power is again relevant.

3. Univariate analyses

Table 4 shows mean abundances of total epifauna and of key taxa contributing to differences amongst assemblages for the three treatments for each collection, along with ANOVA and TUKEY's results. At each collection, the total abundances of epifauna differed significantly among the three treatments, being highest in treatment C, intermediate in treatment P, and lowest in treatment R. The same pattern was found in abundances of the most prominent taxon contributing to differences in assemblages in each collection (Embiez, amphipods; Diana-Night, gastropods; Diana-Day, harpacticoids), and in several other taxa. Some taxa showing significant differences among treatments had a similar trend, but treatment P was not significantly different from either C or R. TUKEY's test failed to detect any pairwise differences in anemone numbers despite a significant ANOVA result. This reflects the infrequent occurrence of anemones in treatments P and R. The total numbers of anemones caught were as follows: C, 11; P, 2; R, 2. Still other taxa did not differ significantly among treatments according to ANOVA results. The overall pattern of abundances in each collection is of decreasing abundance from C to P to R.

Mean biomass of total epifauna and of key taxa are shown for each collection in Table 5. Differences in total biomass among treatments were significant at all collections. At Embiez and Diana-Night, biomass in treatment C was higher than in R, and biomass in P was intermediate but not significantly different from either C or R. At Diana-Day, biomass was significantly higher in C than in P and R, which were not significantly different from each other. Several key taxa showed significant differences, although others did not. At all collections, the general pattern of decreasing biomass from C to P to R is evident but is less marked for total epifaunal biomass than for abundances.

Table 3. Results of ANOSIM comparisons amongst epifaunal assemblages from the three collections. Global test is for any differences amongst treatments, and pairwise tests are for differences between pairs of treatments. Significance level for each comparison is 0.05 (ns = not significant). Contributing taxa are those making a consistently large contribution to differences between samples from the two treatments, listed in order of decreasing importance.

variable	global ANOSIM result	pairwise ANOSIM results	main contributing taxa
EMBIEZ			
abundance	<0.001	C,P0.017 C,R0.004 P,R0.009	Amp, Pol, Gas, Har Amp, Har, Pol Amp, Cal, Har, Mys
biomass	0.001	C,P0.1ns C,R0.002 P,R0.006	Pol, Har, Tan, Amp, Cal Har, Amp, Pol Amp, Har, Cal, Mys, Gas
DIANA-NIGHT			
abundance	<0.001	C,P0.002 C,R0.002 P,R0.002	Har, Tan, Pol, Gas, Amp Gas, Iso, Cal, Har Gas, Amp, Tan, Cal, Har
biomass	<0.001	C,P0.002 C,R0.002 P,R0.002	Har, Chi, Ane Gas, Har, Iso, Cal Gas, Cal, Tan, Amp
DIANA-DAY			
abundance	0.001	C,P0.086ns C,R0.029 P,R0./0.057ns	Har, Tan, Pol Har, Amp, Pol Biv, Amp, Pol
biomass	0.001	C,P0.029 C,R0.029 P,R0.086ns	Tan, Har, Biv Har, Biv, Pol, Gas Pol, Por, Har

4. Size of animals from different habitats

At all collections the pattern of decreasing abundance from C to P to R was stronger than the pattern for biomass. This implies that the average weight of individual animals increased from C to P to R. The mean biomass of individuals in each sample was calculated by dividing the total biomass of a sample by the total number of individuals in the sample. The mean biomass of individuals at each location was lower in habitat C than in the other two habitats, but differences were not significant (Embiez - C: mean = 15.8 μg , (SE = 2.3); P: 18.0(3.3); R: 18.9(4.7); ANOVA, $P = 0.945$. Diana-Night - C: 25.9(3.6); P: 34.1(4.7); R: 33.2(4.6); ANOVA, $P = 0.404$. Diana-Day - C: 19.7(2.5); P: 24.4(3.4); R: 26.0(9.2); ANOVA, $P = 0.860$).

Table 4. Abundances of total epifauna and key taxa in each treatment at the three collections. Numbers are means with standard errors in parentheses. ANOVA results are probabilities; ns = not significant. TUKEY's results show significant differences as letters not grouped by underlining: C = control, P = partly cut, R = removed.

	control	partly cut	removed	ANOVA result	TUKEY's results
EMBIEZ					
all species combined	838 (45)	509 (43)	256 (34)	<0.001	C P R
amphipods	64 (8)	28 (2)	10 (2)	<0.001	C P R
tanaisids	23 (6)	112 (3)	3 (1)	0.011	<u>C P R</u>
harpacticoids	548 (35)	319 (34)	153 (20)	<0.001	C P R
calanoids	15 (4)	19 (3)	22 (9)	0.689ns	
mysids	8 (5)	3 (1)	3 (2)	0.358ns	
polychaetes	135 (14)	78 (6)	49 (7)	<0.001	<u>C P R</u>
gastropods	15 (4)	4 (1)	3 (2)	0.046	
DIANA-NIGHT					
all species combined	2554 (314)	912 (57)	521 (59)	<0.001	C P R
amphipods	187 (22)	86 (10)	30 (4)	<0.001	C P R
tanaisids	197 (41)	49 (6)	15 (2)	<0.001	C P R
isopods	2 (1)	1 (0)	0 (0)	0.003	<u>C P R</u>
harpacticoids	1395 (117)	537 (28)	313 (30)	<0.001	C P R
calanoids	16 (4)	5 (2)	0 (0)	<0.001	C P R
polychaetes	569 (135)	140 (13)	78 (9)	<0.001	C P R
gastropods	11 (2)	3 (1)	0 (0)	<0.001	C P R
anemones	2 (1)	0 (0)	0 (0)	0.045	<u>C P R</u>
chironomids	29 (14)	1 (0)	1 (1)	<0.001	C P R
DIANA-DAY					
all species combined	2308 (625)	451 (87)	143 (20)	<0.001	C P R
amphipods	141 (65)	49 (16)	3 (2)	0.001	<u>C P R</u>
tanaisids	64 (28)	10 (2)	2 (2)	0.028	<u>C P R</u>
harpacticoids	1414 (304)	248 (42)	95 (15)	<0.001	C P R
porcellids	52 (27)	35 (15)	6 (3)	0.493ns	
polychaetes	391 (149)	73 (24)	19 (3)	0.006	<u>C P R</u>
gastropods	27 (15)	3 (3)	2 (2)	0.056ns	
bivalves	34 (30)	11 (5)	1 (1)	0.131ns	

5. Location differences

The two-dimensional ordination plots of assemblages based on abundance and biomass from all collections show strong grouping of treatments within collections, as expected from individual ordinations, but there is also an overriding separation of collections (Fig. 5). In plots for both abundance and biomass, treatment groups from Embiez are distinct but close together, and are all entirely separate from those of Diana. Diana-Night and Diana-Day positions overlap, but Diana-Night

Table 5. Biomasses (AFDW in mg) of total epifauna and key taxa in each treatment at the three collections.

Numbers are means with standard errors in parentheses. ANOVA results are probabilities; ns = not significant. TUKEY's results show significant differences as letters not grouped by underlining: C = control, P = partly cut, R = removed.

	control	partly cut	removed	ANOVA result	TUKEY's results
EMBIEZ					
all species					
combined	13.4 (2.1)	8.9 (1.6)	4.3 (0.9)	0.004	<u>CPR</u>
amphipods	4.2 (0.8)	2.2 (0.5)	0.3 (0.1)	<0.001	<u>CPR</u>
tanais	1.9 (0.6)	0.8 (0.3)	0.3 (0.1)	0.051ns	
harpacticoids	2.1 (0.2)	1.3 (0.3)	0.5 (0.1)	<0.001	CPR
calanoids	0.1 (0.0)	0.1 (0.0)	0.2 (0.1)	0.431ns	
mysids	0.3 (0.1)	0.5 (0.3)	0.1 (0.1)	0.296ns	
polychaetes	2.5 (0.3)	1.0 (0.1)	0.6 (0.1)	<0.001	<u>CPR</u>
gastropods	0.4 (0.1)	1.2 (0.5)	0.1 (0.0)	0.059ns	
DIANA-NIGHT					
all species					
combined	67.9 (16.7)	31.3 (5.4)	18.4 (3.9)	0.002	<u>CPR</u>
amphipods	16.9 (2.9)	7.8 (1.3)	2.9 (0.5)	<0.001	CPR
tanais	11.4 (4.1)	3.3 (0.2)	1.0 (0.5)	>0.001	CPR
isopods	0.8 (0.3)	0.1 (0.1)	0.0 (0.0)	0.003	CPR
harpacticoids	3.8 (0.4)	1.5 (0.1)	0.8 (0.1)	<0.001	CPR
calanoids	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.058ns	
polychaetes	12.8 (4.0)	3.7 (0.8)	3.0 (0.6)	0.001	CPR
gastropods	4.8 (1.1)	1.5 (0.5)	0.0 (0.0)	<0.001	CPR
anemones	1.5 (0.3)	0.0 (0.0)	0.1 (0.1)	<0.001	CPR
chironomids	0.8 (0.5)	0.0 (0.0)	0.0 (0.0)	0.028	<u>CPR</u>
DIANA-DAY					
all species					
combined	44.9 (11.2)	11.0 (2.4)	3.6 (1.2)	0.001	<u>CPR</u>
amphipods	15.4 (7.9)	3.1 (1.2)	0.4 (0.2)	0.025	<u>CPR</u>
tanais	3.2 (1.1)	0.3 (0.1)	0.2 (0.1)	0.022	<u>CPR</u>
harpacticoids	5.4 (1.4)	0.8 (0.2)	0.2 (0.1)	<0.001	CPR
porcellids	0.2 (0.1)	0.2 (0.1)	0.0 (0.0)	0.194ns	
polychaetes	6.4 (2.2)	1.0 (0.2)	0.2 (0.1)	0.007	<u>CPR</u>
gastropods	2.6 (1.1)	1.7 (1.2)	0.0 (0.0)	0.115ns	
bivalves	0.5 (0.1)	0.3 (0.3)	0.0 (0.0)	0.124ns	

treatment groups, whilst distinct, are close together, whereas Diana-Day treatment groups are more widely spread. Although the spacing amongst treatment groups is different for Diana-Night and Day, the effect of partly cutting and removing seagrass was the same, with groups, C, P, and R positioned in that order along a straight line gradient. This gradient is also evident for Embiez treatment groups. Differences amongst treatments and collections were statistically significant (Table 6). ANOSIM comparisons between pairs of treatments were all significant but are

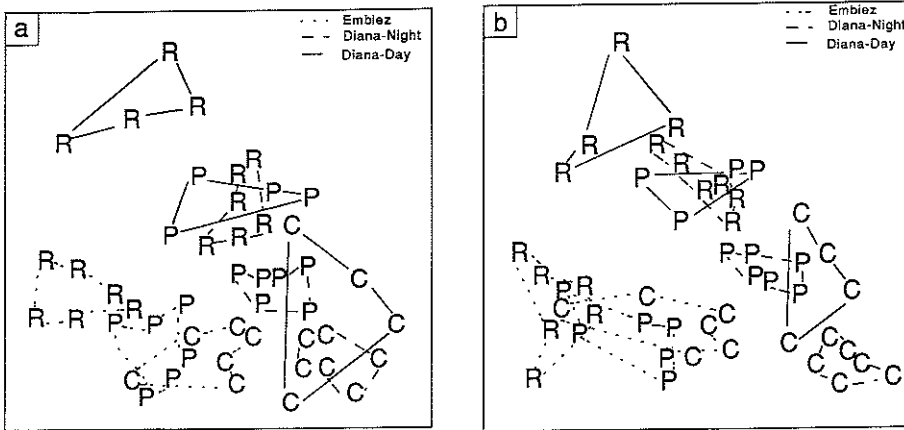


Fig. 5. Two-dimensional MDS ordination plots of epifaunal assemblages from all collections based on a. abundance (stress = 0.123) and b. biomass (0.124) data. C = control; P = partly cut; R = removed.

Table 6. Results of two-way crossed ANOSIM comparisons amongst epifaunal assemblages of collections and treatments.

Global test is for differences amongst treatments or collections, as specified. Pairwise tests for treatments were all significant but are not shown. Pairwise test amongst collections are shown. Significance level for each comparison is 0.05. Contributing taxa are those making a consistently large contribution to differences between samples from the two collections, listed in order of decreasing importance. EM = Embiez, DN = Diana-Night, DD = Diana-Day.

variable	global ANOSIM result	pairwise ANOSIM results for collection	main contributing taxa
abundance	treatments < 0.001	EM, DN < 0.001	Por, Biv, Mys
	collection < 0.001	EM, DD < 0.001	Cal, Cyc, Pol, Har
		DN, DD < 0.001	Cyc, Pol, Har
biomass	treatments < 0.001	EM, DN < 0.001	Por, Mys, Biv, Gas, Pol
	collection < 0.001	EM, DD < 0.001	Cal, Cyc, Mys, Pol, Har, Gas
		DN, DD < 0.001	Cyc, Har, Pol

not shown in Table 6 because they have been reported for each location separately. Pairwise comparisons amongst collections were all significant on both abundance and biomass data; that is, after taking into account treatment differences, assemblages from all three collections were significantly different from each other.

Results of two-factor ANOVA tests on collection and treatment for abundance and biomass data are presented in Table 7. Significant interaction was detected on abundance data, so that probabilities for main effects should be treated with caution. Given the interaction, TUKEY's tests are best used to compare pairwise differences amongst collections separately for each treatment. Total abundances were higher at Diana-Night than at Embiez for each treatment. Diana-Day abundances were similar to those at Diana-Night in treatment C, but were similar to those at Embiez in treatment P and even lower than those at Embiez in treatment R.

Table 7. Total epifaunal abundance and biomass comparisons across collections. Results shown as probabilities for two factors and interaction term in two-way ANOVA. TUKEY's results for collection only, separately for each treatment, show significant differences as letters not grouped by underlining. EM = Embiez, DN = Diana-Night, DD = Diana-Day.

	term	ANOVA result	treatment	TUKEY's results for collection comparisons
abundance	treatment	<0.001	C	<u>DN DD EM</u>
	collection	<0.001	P	<u>DN EM DD</u>
	interaction	<0.001	R	<u>DN EM DD</u>
biomass	treatment	<0.001	C	<u>DN DD EM</u>
	collection	<0.001	P	<u>DN DD EM</u>
	interaction	0.057	R	<u>DN EM DD</u>

The interaction term in the ANOVA test on biomass data was close to significance ($P = 0.057$). Again it is informative to make pairwise TUKEY comparisons of collections separately for each treatment. Total biomass was higher at Diana-Night than at Embiez for each treatment. Biomass at Diana-Day was similar to that at Diana-Night in treatment C, but was similar to that at Embiez in treatments P and R.

Discussion

The epifauna sampled in the three experimental treatments was different whether measured as abundance or biomass. At both sites, total abundance and biomass within treatments declined in line with decreasing canopy height. Epifaunal assemblages differed amongst treatments, and the directions of differences, but not their magnitudes, were consistent at the two sites and at the night and day sampling. At both sites, the same taxa tended to be dominant numerically and by weight, although the importance of these taxa in distinguishing amongst treatments varied with location. These dominant taxa showed a very strong pattern of decreasing abundance and biomass from treatment C to P to R. As a result, the total abundance and biomass declined from C to P to R.

These patterns in epifaunal abundance can be explained in terms of animals selecting habitat (STONER, 1980; LEBER, 1985; BELL & WESTOBY, 1986b, c), but the present results cannot separate this explanation from others. The behavioural mechanism of habitat selection is assumed to be a response to the habitat itself, but the underlying advantage might be in terms of any of several factors, including increased living space and food availability (LEBER, 1985). It is equally possible that animals may respond directly to such factors. Reduction in seagrass cover may, for example, have lessened the amount of food available to epifauna (food includes any or all of the following: detritus, bacteria, microscopic algae, and perhaps some of the smaller invertebrates themselves). Movement to find food is not the same thing as habitat selection, but it may result in occupation of habitat that supports more food. Other possible explanations for the lower abundance of epifauna with decreasing seagrass cover are (as listed by LEWIS (1984)): 1) less

dampening of hydrodynamic forces; 2) decreased number of microhabitats; 3) less stabilisation and deposition of sediment. A treatment not used in the present study, that of patches unvegetated prior to the experiment, could be usefully employed to help distinguish among some of the above explanations. CONNOLLY (1995b) has shown, for example, that epifaunal abundances in patches from which seagrass had been removed did not match those from patches devoid of vegetation prior to the experiment.

The pattern of decline from C to P to R was less obvious in biomass data than in abundance data. Although differences in mean biomass of individuals were not significant, at each location mean biomass was lowest in habitat C. This can be taken as weak evidence that the relative importance of heavier animals was greater in plots in which seagrass cover was reduced. There are many possible explanations for any increased importance of heavier animals in habitats from which vegetation had been removed. Predators may have removed animals differentially according to size, or the food resource available in modified habitats may have been more attractive to larger animals. The responses to reduced canopy could be instinctive selection of habitat. An alternative explanation for the increased dominance of larger animals with decreasing canopy cover is that heavier animals, either because of their weight or because they are more powerful swimmers, may have been less likely to be removed along with the vegetation at the time of cutting. If smaller animals removed accidentally along with vegetation had not returned by the time epifauna was collected, then the relative importance of heavier animals would increase with the amount of vegetation removed. Perhaps the most likely explanation for the larger average size of individuals in clipped plots is that the leaf tips had been removed, and these may provide a microhabitat frequented more by lighter animals.

The differences amongst treatments involved the abundance or biomass of taxa, not the presence or absence of taxa. This result may reflect the gross clumping of species and possibly of functional groups into single, higher taxa, so that changes in the fauna at those levels would not have been detected. Nevertheless, WARWICK (1988) showed that multivariate analyses at family level reproduced very closely the results obtained at species level, and even analyses at the level of phylum generally agreed surprisingly well with those at lower taxonomic levels. The significant differences detected among epifaunal assemblages from different treatments demonstrate that the taxa used in this study were adequate to examine the general question posed about the effects of canopy reduction on epifauna. There remains an opening, nevertheless, for further manipulative experiments in which invertebrates are identified at lower taxonomic levels.

The epifauna of Embiez and Diana-Night was consistently different. Multivariate analysis showed no overlap of assemblages from the two collections. Epifaunal abundance and biomass were always higher at Diana in all treatments, and Embiez was more characterised by greater abundance of lighter animals in all treatments. Plausible explanations can be proposed for these differences, for example in terms of pollution at the Embiez location. However, we shall not discuss them further because the comparison between locations is confounded with time; there was a 10-day period between the experiments at the two locations. The differences suggest topics for further research.

Although the fauna at the two sites differed, the effects of partly cutting or totally

removing the seagrass canopy were the same at both sites. Treatment groups in the ordination plots based on abundance and biomass were related in the same way at the two sites, and the differences among treatments in abundance and biomass were also consistent.

Differences between night and day collections at Diana are confounded with time. We note the differences here, but leave their interpretation to further work designed for the purpose. Modifying seagrass canopy had the same type of effect on day and night fauna, but the magnitudes of those effects differed. Treatment groups on the ordination plots for day fauna were more spread-out than for night fauna. Abundance of day fauna matched that of night fauna in control plots, but was as low as that at Embiez in modified treatments.

The results presented here can be combined with results from the fish studies of BELL & WESTOBY (1986a, b, c), BELL *et al.* (1987) and JENKINS *et al.* (in press) to sharpen explanations of fish distributions. The control and shortened canopy treatments in this study were similar to the control and shortened treatments shown by BELL & WESTOBY (1986c) to affect fish abundances, and the seagrass in their study (*Zostera capricorni*) is similar in height, width, density, and general form to the seagrass (*Cymodocea nodosa*) in the present study. Fish communities of south eastern Australia are also similar to those of the Mediterranean region at familial level (POLLARD, 1984). Given that small fish in shallow, sheltered water bodies feed predominantly on epifaunal invertebrates (BELL & HARMELIN-VIVIEN, 1983; CASABIANCA & KIERNER, 1969; DUKA, 1978; KHOURY, 1984; KLUMPP *et al.*, 1989), the current results are consistent with a model in which fish abundances in areas with different levels of seagrass cover are explained by food availability (CONNOLLY, 1994b, c, d; JENKINS *et al.*, in press), although critical experiments remain to be done.

Summary

The main aim of this study was to determine whether alterations to the seagrass canopy affected epifaunal abundance and community structure. Epifaunal assemblages were altered upon the reduction of canopy height, in a similar fashion at both sites, and at night and day at Diana. The total abundance and biomass of epifauna, and of key taxa, were reduced in line with reduction in canopy height.

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