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Predicting understory structure from the presence and composition of canopies: an assembly rule for marine algae

Received: 16 June 2004 / Accepted: 2 February 2006 / Published online: 24 February 2006
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Abstract Assembly rules provide a useful framework for predicting patterns of community assembly under defined environmental conditions. Habitat created by canopy-forming algae (such as kelps) provides a promising system for identifying assembly rules because canopies typically have a large and predictable influence on understory communities. Across >1,000 km of subtidal South Australian coastline, we identified natural associations between assemblages of understory algae and (1) monospecific canopies of *Ecklonia radiata*, (2) canopies comprised of *E. radiata* mixed with Fucales (*Cystophora* spp. and *Sargassum* spp.), and (3) gaps among canopies of algae. We were able to recreate these associations with experimental tests that quantified the assembly of understory algae among these three habitat types. We propose the assembly rule that understory communities on subtidal rocky coast in South Australia will be (1) monopolised by encrusting coralline algae beneath monospecific canopies of *E. radiata*, (2) comprised of encrusting corallines, encrusting non-coralines, and sparse covers of articulated corallines, beneath mixed *E. radiata*-Fucales canopies, and (3) comprised of extensive covers of articulated corallines and filamentous turfs, as well as sparse covers of foliose algae and juvenile canopy-formers, within gaps. Consistencies between natural patterns and experimental effects demonstrate how algal canopies can act as a filter to limit the subsets of species from the locally available pool that are able to assemble beneath them. Moreover, the subsets of

species that assemble to subtidal rocky substrata in South Australia appear to be predictable, given knowledge of the presence and composition of canopies incorporating *E. radiata*.

Keywords Association · Benthos · *Ecklonia radiata* · Habitat heterogeneity · Kelp

Introduction

A fundamental goal of ecology is to derive testable predictions about the causes of patterns in nature (Underwood 1997). An enduring criticism of community ecology centres on the apparent lack of general models that use a few key variables to accurately predict pattern in the assembly of communities (Peters 1991; Keddy 2001). To redress this deficiency, the theory of assembly rules presents a predictive framework to specify a (preferably short) list of key factors that determine which subset of species from the available pool may assemble to a given habitat (Keddy and Weiher 1999). Formally introduced by Diamond (1975), and refined by many since (e.g. Connor and Simberloff 1979; Drake 1990; Weiher and Keddy 1999), assembly rules predict the biological and physical “filters” (sensu Keddy 1992) that allow some species to contribute to community assembly, while preventing others. Knowledge of the precise mechanisms driving such effects (e.g. specific dispersal constraints, environmental constraints, and internal dynamics: Belyea and Lancaster 1999) may help us understand exactly why particular communities assemble the way they do. However, such information is not always necessary to accurately predict when and where such communities will assemble (i.e. to give the assembly rule predictive power: Keddy 1992). Although assembly rules present an attractive opportunity to develop and refine predictive models about the structural dynamics of communities, empirical examples of explicitly stated rules are rare (but see Belyea and Lancaster 1999; Keddy and Weiher 1999).

Communicated by Christian Koerner

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For generations, ecologists have debated whether plant communities represent repeatable associations structured by interdependence among species, or merely coincidental collections of taxa with similar adaptations to the abiotic environment (e.g. Clements 1916; Gleason 1926; Whittaker 1951; Callaway 1997). A remarkable quantity of observational and experimental evidence demonstrates interdependence among plant species, manifest through numerous positive (e.g. facilitation: Callaway 1995) and negative interactions (e.g. competition: Grace and Tilman 1990). Where the presence of one species facilitates or suppresses the distribution and abundance of others, such interactions may effectively direct the assembly of the community, and therefore represent an assembly rule for that particular community. Assembly rules are thought to occur in plant communities (Díaz et al. 1998; Cody 1999), but have been considered by some to be difficult to detect because of subtle effect sizes and large variation in natural systems (e.g. Wilson 1999).

Habitat created by canopy-forming vegetation provides a promising system to identify assembly rules because canopies typically have a large influence on the distribution and abundance of understory flora (Grime 1979; Callaway 1995; McPherson and Weltzin 1998). Such effects involve numerous biotic (e.g. toxins) and abiotic factors (e.g. shade), and are often so strong that functional groups of understory taxa have been identified on the basis of their association with the canopy (e.g. shade-tolerant vs. shade-intolerant; Whitmore 1989). Subtidal canopies of algae (e.g. kelp forests) form one of the most extensive marine habitats at temperate latitudes, and frequently coexist with understory algae (e.g. encrusting and articulated coralline algae) that differ greatly from those observed within gaps among canopies (e.g. filamentous and foliose algae) (Kennelly 1987; Chapman and Johnson 1990; Irving et al. 2004b). Such differences are commonplace both in the presence and absence of intense grazing pressure from herbivorous invertebrates (e.g. urchins) (Fowler-Walker and Connell 2002). Experimental removal of canopies typically results in changes to the structure of the understory community such that they become more similar to those naturally observed within gaps (Kennelly 1987; Edwards 1998; Melville and Connell 2001), with such observations highlighting a clear influence of canopies on the assembly of understory. As such, rules for the assembly of understory may be broadly based on the presence or absence of canopies.

Heterogeneity in the structure of understory communities is not just associated with the presence or absence of canopies, but also with variation in the composition of canopies. Broadly, canopy-forming algae can exist in monospecific stands and also as mixed-species aggregations (Dayton et al. 1984; Goodsell et al. 2004). Even at this coarse level of classification, large differences are often observed in the structures of understory communities (Irving et al. 2004b). Therefore, it is possible that more sophisticated rules of assembly for

understorey could be proposed when the composition of canopies is considered additional to their presence. Few studies have addressed this possibility because research efforts around the world have largely focused on understanding the responses of understory to the presence or absence of canopies per se, where variation in the composition of canopies is rarely described (Goodsell et al. 2004). Such knowledge is worth pursuing, however, given that both monospecific and mixed-species stands of canopy-forming algae create conspicuous subtidal habitats on temperate rocky coasts (Dayton et al. 1984; Goodsell et al. 2004).

The specific mechanisms that drive rules for the assembly of understory algae are likely to involve numerous physical factors modified by canopies (e.g. light intensity: Edwards 1998; Connell 2003, water flow: Jackson and Winant 1983; Duggins and Eckman 1994). Close agreement has previously been observed between natural patterns of understory structure (e.g. canopies vs. gaps) and results of experimental tests of particular factors on understory (e.g. shade vs. no shade: Kennelly 1989; Connell 2003). This knowledge has contributed greatly to a mechanistic understanding of how canopies of algae can act as filters to facilitate or suppress species from the understory (Dayton 1975; Bertness et al. 1999; Connell 2003). Importantly, such information is likely to improve the predictive capacity of assembly rules for understory algae by helping us to better understand the causes of natural variability in the structure of understory communities (e.g. Irving et al. 2004b).

The subtidal rocky coasts of temperate Australia support extensive covers of the canopy-forming Laminarian alga *Ecklonia radiata* (C. Agardh) J. Agardh, which can persist in dense monospecific stands or as mixed-species aggregations with canopy-forming species of Fucales (*Cystophora* spp., *Sargassum* spp. etc) (Shepherd and Womersley 1970; Goodsell et al. 2004). Additionally, canopies are frequently punctuated by gaps created by wave energy during storms (Kennelly 1987). We identified the nature of differences in the structure of assemblages of understory algae among monospecific stands of *E. radiata*, stands of *E. radiata* mixed with Fucales, and gaps, across >1,000 km of continuous coastline in South Australia. We then assessed whether we could experimentally recreate these patterns by testing the hypothesis that the observed differences on natural reef occur because of the presence of habitat-type; monospecific *E. radiata*, mixed *E. radiata*-Fucales, or gaps. If supported, such knowledge would provide a foundation for proposing rules of assembly based on the presence and composition of canopies incorporating *E. radiata* in South Australia. Although a mechanistic understanding of such assembly rules was beyond the scope of this study, we provide a framework for such research by testing for differences in the intensity of four physical variables (light, sedimentation, water flow, and lamina abrasion) among all three habitats.

Materials and methods

Natural canopy–understorey associations

Assemblages of understorey algae were quantified across >1,000 km of continuous South Australian coastline during the austral summer of 2001/2002. Four locations, each separated by at least 100 km, were randomly chosen from areas of coast exposed to the predominant swell. Within each location, four sites were randomly chosen (each separated by one to ten km). At each site, understorey algae (<5 cm in height) were quantified from monospecific stands of *E. radiata*, stands of *E. radiata* mixed with Fucales, and gaps among stands of canopy-forming algae [experimental design: habitat × site(location)]. Habitats were identified on a scale of 1 m² as (1) monospecific *E. radiata* where ≥80% of the canopy cover was *E. radiata*, (2) mixed *E. radiata*-Fucales where 40–60% of the canopy cover was *E. radiata*, with the remaining cover consisting of canopy-forming species of Fucales (e.g. *Cystophora* spp., *Sargassum* spp.), and (3) gaps among canopies of algae where rocky substrata did not support canopy-forming algae > 5 cm in height (Irving et al. 2004b). The abundance (percentage cover) of understorey algae within each type of habitat was quantified using the point intercept method (25 regularly spaced points in a 0.2×0.2 m quadrat, *n* = 8 per habitat). Replicates were separated by 4–10 m and sampling was done between 3 and 10 m depth at all sites.

Understorey algae were quantified as morphological groups: encrusting coralline algae, encrusting non-coralline algae, filamentous turf-forming algae, articulated coralline algae, foliose (fleshy, non-coralline) algae and juvenile stages of canopy-forming algae, after Steneck and Dethier (1994). A test for multivariate differences in the structure of understorey assemblages among habitats, sites and locations was done using a mixed-model three-way permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). Data were fourth-root transformed with permutation of residuals (reduced model) done using Bray–Curtis distance measures. Non-metric ordination plots were constructed to represent multivariate patterns, using similarity values calculated from Bray–Curtis distances. Similarity percentages (SIMPER) were used to identify the contribution of each group of understorey algae to the multivariate differences among habitats (Clarke and Warwick 1994). Tests for differences in the percentage cover of individual morphological groups were done using ANOVA. For all analyses, “location” was treated as random, “site” was treated as random and nested within “location”, and “habitat” was treated as fixed and orthogonal.

Experimental assembly of understorey

Experimental reefs were constructed at West Island, South Australia, in December 2002 to represent the

three habitats sampled across South Australia (monospecific *E. radiata*, mixed *E. radiata*-Fucales, and gaps; *n* = 7 per habitat). Granitic boulders colonised by algae were collected from a natural boulder reef (Spit reef) and were translocated into plastic crates (0.57 m long × 0.65 m wide × 0.10 m high) located adjacent to Spit reef at 5 m depth. Boulders supporting adult *E. radiata*, *Cystophora* spp. or *Sargassum* spp. were used to construct reefs designated as monospecific *E. radiata* or mixed *E. radiata*-Fucales, while boulders that did not support canopy-formers were used to construct reefs designated as gaps. All boulders used to construct gaps were collected from beneath canopies of algae. When all experimental reefs were constructed, a granite boulder (20–25 cm diameter) devoid of visible life was taken from above the intertidal region of West Island and placed at the centre of each reef. The algae recruiting to this boulder were sampled at least monthly over 357 days using the point intercept method (25 regularly spaced points in the central 0.1×0.1 m of each boulder) and according to the morphological groups described above. Experimental reefs were separated by 2–5 m, with treatments maintained on a monthly basis by replacing lost or damaged canopy-forming algae with healthy individuals from Spit reef, and by removing juvenile canopy-formers recruiting to reefs designated as gaps. Single-factor multivariate (PERMANOVA) and univariate analyses (ANOVA) were done for the final day of sampling (357th day).

There was potential for pre-existing conditions on each reef (i.e. the type of algae growing on boulders used to construct the reefs) to bias the assembly of algae on the bare boulders and confound our interpretation of differences among habitats. All reefs were constructed with boulders collected from beneath natural canopies, which ensured the pool of potential colonists on experimental reefs at the start of the experiment were locally (i.e. within each reef) consistent among treatments. Moreover, spores of marine algae generally disperse over distances of up to tens of metres (Santelices 1990), meaning that the pool of potential colonists likely extended far beyond that produced locally (i.e. by algae growing on neighbouring boulders within each experimental reef). Even so, the process of translocating boulders from natural to experimental reefs has the potential to affect the algae growing on them (i.e. potential colonists) and also bias the results. Such effects were considered unlikely, however, because previous tests for artefacts associated with the translocation of boulders (vertical and horizontal disturbance) on understorey algae at this location have consistently yielded non-significant results (e.g. Irving and Connell, *Mar Ecol Prog Ser*, in review).

Quantification of the physical environment

Four environmental variables (light intensity, sedimentation regime, water flow and lamina abrasion) were

quantified among all three habitats to provide observations for mechanistic models of proposed assembly rules. The intensity of light ($\mu\text{E m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation: 400–700 nm) reaching the understory was quantified in each habitat using an underwater quantum sensor (LI-192SA, Li-Cor, Lincoln, NE, USA) and surface meter (LI-250) on a cloudless day. Five experimental reefs were randomly selected from the seven available replicates of each habitat, and five measurements of light intensity (each averaged over 15 s) were taken on each reef. The mean and variance observed among replicate readings on each reef were analysed separately to test for differences in the average light intensity and variation in light intensity among habitats. All measurements were taken within 1 h (30 min each side of solar noon).

Differences in the rate of deposition of sediments (organic and inorganic particles $< 1 \text{ mm}^2$) among habitats were tested using cylindrical sediment traps (170 mm high \times 50 mm diameter) secured to experimental reefs ($n = 5$ per habitat). Traps were deployed on two occasions (once for 15 days and once for 4 days). To relate the rate of sediment accumulation on boulders to the depositional environment, accumulated sediments were resuspended and cleared away from boulders before traps were deployed, by gently increasing water motion over the surfaces of boulders (via a waving motion with one hand). When traps were collected, the amount of sediment that had accumulated on the upward-facing surfaces of boulders was sampled by vacuuming an area of 5 \times 5 cm using a syringe. Both deposited and accumulated sediments were oven-dried at 70 °C for 48 h before being weighed (mass (g) per m^2 per day). The amount of accumulated sediment was further analysed as a percentage of that deposited on each reef.

Quantifying both water flow beneath canopies and abrasion of the substratum by canopies can be problematic because abrasion is not independent of flow (i.e. flow causes canopies to abrade). We estimated flow and abrasion in each habitat by measuring the amount of dissolution of plaster clods, followed by a series of analyses to tease apart the amount of plaster lost due to flow from that lost due to abrasion. Fifteen clods were placed within each habitat and were evenly partitioned among three treatments: (1) no cage (exposed to flow and abrasion), (2) full cage (protected from abrasion but exposed to flow), and (3) partial cage as a procedural control (exposed to abrasion and flow). Cages were constructed from 50 \times 50 mm galvanised steel mesh, with partial cages consisting of a base and all four sides but no roof, which exposed clods to abrasion in the presence of a cage structure (experimental design: 3 habitat \times 3 cage = 9 treatment levels, $n = 5$). All clods were oven-dried (70 °C for 48 h) and weighed prior to placement among experimental treatments, and again after three days of submergence, with the amount of plaster lost from each clod calculated as a percentage of the original mass.

Analyses proceeded in four steps. First, we tested for artefacts of cages on flow by comparing among all three

“cage” treatments in gaps only (no artefacts were detected). It was not possible to test for this artefact beneath canopies since clods were exposed to both flow and abrasion. Assuming that cages did not alter the flow beneath canopies either, we (second) tested for differences in flow among habitats by comparing the percentage loss of plaster from clods that were fully caged in each habitat (i.e. clods protected from abrasion but exposed to flow). Third, we tested for artefacts of cages on the loss of plaster beneath canopies (i.e. the percentage lost due to the combined effect of flow and abrasion beneath canopies) by comparing uncaged clods with those that were partially caged (no artefacts were detected). Fourth, differences in abrasion among habitats were tested by subtracting the percentage loss of plaster from fully caged treatments (absence of abrasion but presence of flow) from the percentage loss of plaster from uncaged treatments (presence of abrasion and flow). For this final analysis, replicate values were obtained by randomly pairing uncaged replicates with fully caged replicates for each habitat ($n = 5$).

Results

Multivariate differences among habitats

Assemblages of understory algae differed among all three habitats on natural reef across South Australia (Table 1), with results from experimental reefs consistent with this widespread pattern (PERMANOVA: $F_{2,18} = 116.95$, $P < 0.001$, gap \neq mixed \neq monospecific; Fig. 1). On natural and experimental reefs, understory assemblages beneath mixed and monospecific canopies were more similar to each other than to assemblages in gaps (smaller t -values for comparison of mixed vs. monospecific than for either mixed vs. gap or monospecific vs. gap, Table 1). Moreover, multivariate differences among habitats across South Australia did not vary greatly among locations or sites (Table 1: non-significant habitat \times location and habitat \times site(location) interactions), indicating that local-scale multivariate patterns

Table 1 Result of PERMANOVA testing for differences in the structure of assemblages of understory algae among habitats (monospecific *E. radiata*, mixed *E. radiata*-Fucales, and gaps), locations and sites on natural reef across South Australia

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>
Habitat	2	7.48	18.76	*
Location	3	2.86	15.43	ns
Site(location)	12	0.19	3.64	***
Habitat \times location	6	0.40	6.13	ns
Habitat \times site(location)	24	0.07	1.28	ns
Residual	336	0.05		
Pair-wise tests among habitats	<i>t</i>	<i>P</i>		
Gap vs mixed	7.84	***		
Gap vs monospecific	12.66	***		
Mixed vs monospecific	5.99	***		

* $P < 0.05$, *** $P < 0.001$, ns $P > 0.05$

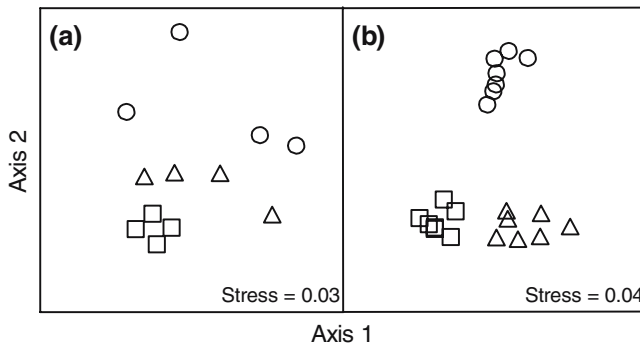


Fig. 1a–b Non-metric ordination of understory assemblages sampled in gaps (*circles*), mixed stands (*triangles*) and monospecific stands (*squares*) of *E. radiata* **a** at four locations across South Australia and **b** on experimental reefs after 357 days. For ease of representation, only a single point for each location \times habitat combination is shown for (**a**), whereas each point represents a single replicate for (**b**). Stress values < 0.2 indicate an interpretable ordination of multivariate data in two-dimensional space (Clarke 1993)

(i.e. differences among habitats within a site) are repeated across a large extent of the coastline of South Australia.

SIMPER analyses revealed that extensive covers of articulated corallines and filamentous turfs, and sparse covers of encrusting corallines, largely distinguished assemblages within gaps from those beneath mixed and monospecific canopies on natural and experimental reefs (Table 2: gap vs. mixed, and gap vs. monospecific). Similarly, greater covers of articulated corallines and encrusting non-corallines primarily distinguished assemblages beneath mixed canopies from those beneath monospecific canopies (Table 2: mixed vs. monospecific). Encrusting non-corallines also contributed to differences between mixed canopies and gaps (Table 2).

Table 2 Summary of SIMPER analyses: percentage contribution of each group of understory algae to the overall dissimilarity between habitats on natural and experimental reefs (pairwise comparisons of gaps, mixed canopies, and monospecific canopies)

	Habitat comparison		
	Gap vs. mixed	Gap vs. monosp.	Mixed vs. monosp.
Natural reef			
Encrusting coralline	16.70	18.48	10.47
Articulated coralline	15.77	18.05	23.01
Filamentous turf	30.57	28.42	13.34
Foliose algae	10.71	10.09	18.51
Encrusting non-coralline	17.73	12.47	19.48
Juv. canopy-formers	8.52	12.50	15.19
Experimental reefs			
Encrusting coralline	22.43	30.56	10.25
Articulated coralline	16.57	22.48	24.18
Filamentous turf	20.57	24.40	0.00
Foliose algae	14.83	17.49	0.00
Encrusting non-coralline	21.25	0.00	65.57
Juv. canopy-formers	4.36	5.06	0.00

Dissimilarities were calculated from Bray–Curtis distance measures

Univariate differences among habitats

We plot natural patterns and experimental effects together (Fig. 2) to assist interpretation of the extent to which experimental effects explain naturally occurring patterns, but analyses were necessarily kept separate due to the differences in sampling design (natural patterns: $n = 128$) and experimental design (experimental effects: $n = 7$). Encrusting coralline algae monopolised space beneath canopies relative to gaps, forming more extensive covers beneath monospecific than mixed canopies on natural (Fig. 2a, Table 3a) and experimental reefs (Fig. 2a, ANOVA: $F_{(2,18)} = 279.88$, $P < 0.0001$, SNK tests for experimental reefs: gap $<$ mixed $<$ monospecific; Table 4). At three of four locations, articulated coralline algae and turfs of filamentous algae on natural reef were more extensive within gaps than beneath canopies (Fig. 2b, c, Table 3b, c). Experimental effects were consistent with this pattern for both groups of algae (Fig. 2b, c, ANOVA for articulated coralline: $F_{(2,18)} = 15.37$, $P < 0.001$; for filamentous turf: $F_{(2,18)} = 41.13$, $P < 0.0001$, SNK tests: gap $>$ mixed = monospecific for both groups; Table 4). Articulated corallines were also more extensive beneath mixed than monospecific canopies at two locations (Yorke and Fleurieu); a pattern that was not observed on experimental reefs (Fig. 2b, Table 4).

Differences in the covers of foliose algae and encrusting non-coralline algae among habitats were spatially variable on natural reef, yet some consistent patterns emerged. Foliose algae were generally more extensive within gaps and beneath mixed canopies than monospecific canopies (but see Eyre East: Fig. 2d, Table 3d), while encrusting non-corallines, although infrequently sampled, were often most abundant beneath mixed canopies (Fig. 2e, Table 3e). On experimental reefs, foliose algae were also abundant within gaps (although not beneath mixed canopies: Fig. 2d, ANOVA: $F_{(2,18)} = 27.50$, $P < 0.0001$, SNK tests: gap $>$ mixed = monospecific; Table 4), with encrusting non-corallines only sampled beneath mixed canopies (Fig. 2e, ANOVA: $F_{(2,18)} = 262.05$, $P < 0.0001$, SNK tests: mixed $>$ gap = monospecific; Table 4). Juvenile canopy-formers were generally more extensive within gaps and beneath mixed canopies than monospecific canopies on natural reef (Fig. 2f, Table 3f), but were rarely sampled on experimental reefs (Fig. 2f, ANOVA: $F_{(2,18)} = 2.37$, $P > 0.12$, SNK tests: gap = mixed = monospecific; Table 4).

Spatial variation of differences among habitats on natural reef was evident for all groups of understory algae. Of 16 sites in total (4 sites \times 4 locations), the number of sites showing patterns inconsistent with that detected at the scale of location was five for encrusting coralline, three for articulated coralline and one for filamentous turf. A greater number of sites were inconsistent for foliose algae (11 sites), encrusting non-corallines (9 sites) and juvenile canopy-formers (13 sites). Among locations, some minor variation of pattern was observed for encrusting and articulated corallines, filamentous turfs, and juvenile canopy-formers (Fig. 2a–c, f, Table 4). Variability of pattern was most

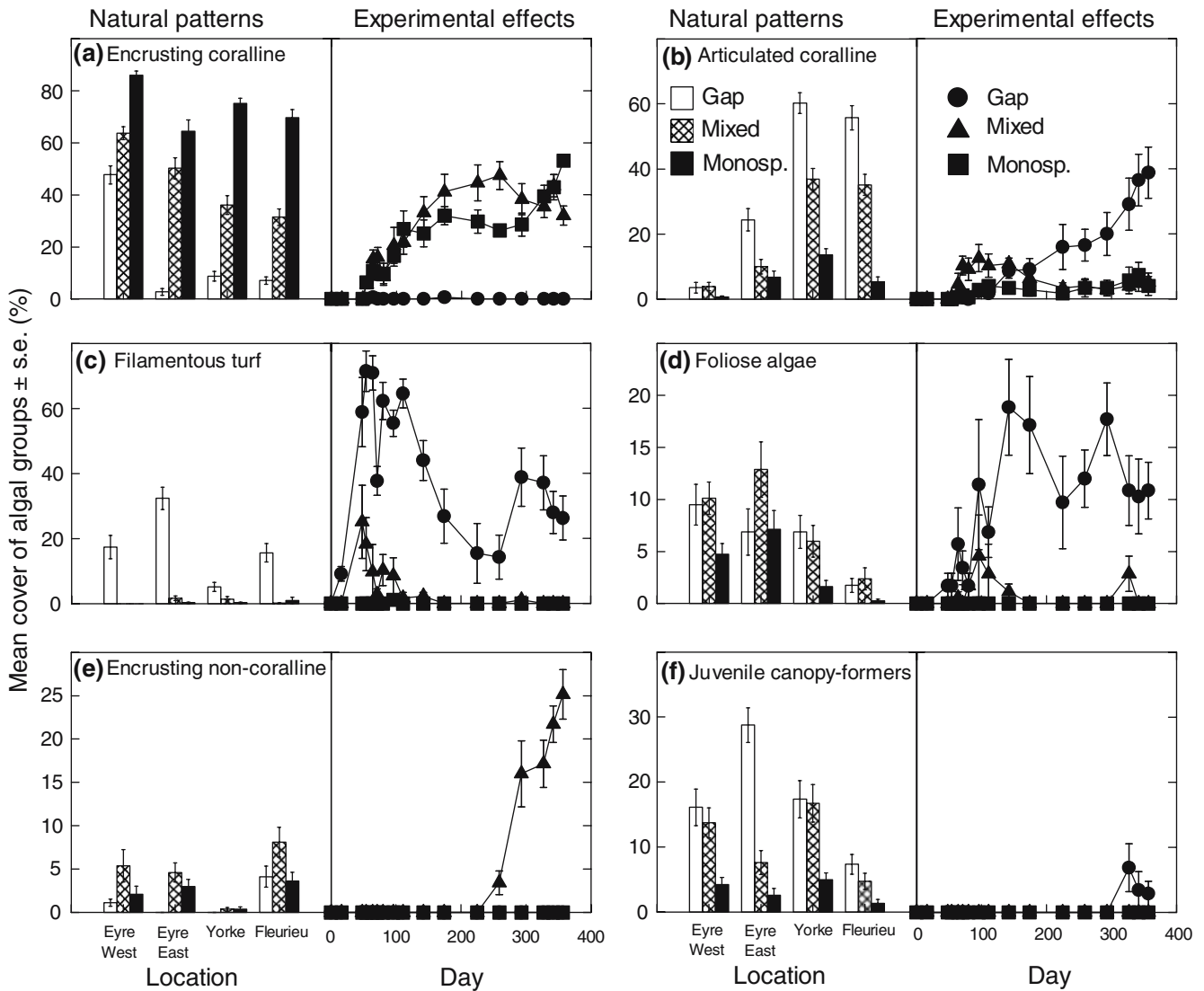


Fig. 2 Mean percentage cover (\pm SE) of morphological groups of algae sampled in gaps, mixed stands and monospecific stands of *E. radiata* at four locations across South Australia (natural patterns) and on experimental reefs over 357 days (experimental effects)

apparent for foliose algae and encrusting non-corallines (Fig. 2d, e, Table 4). Importantly, while we observed such natural variation in patterns among sites and locations, key patterns often emerged that were consistent with experimental effects (Table 4).

Environmental variables

The mean intensity of light reaching the substratum in gaps was greatly reduced by canopies of algae, especially beneath monospecific canopies of *E. radiata* (Fig. 3a, Table 5a). Greatest variability in the light environment occurred beneath mixed canopies and least variability beneath monospecific canopies (Fig. 3b, Table 5b). The rate of sediment deposition did not differ among habitats during each period of sampling (Fig. 3c, d, Table 5c,

d), although greater rates of sediment deposition were observed at time 2 compared to time 1 (probably due to resuspension of sediments by large waves during time 2; A.D. Irving, personal observation). The mass of sediment that accumulated on boulders, and the percentage of deposited sediments that accumulated, was an order of magnitude greater in gaps than beneath canopies, while mixed canopies also accumulated greater amounts than monospecific canopies (Fig. 3e, f, Table 5e, f).

No artefacts associated with the structure of cages were detected for water flow within gaps (ANOVA: $F_{(2,12)}=1.16$, $P>0.34$) or for the percentage loss of plaster beneath mixed and monospecific canopies (ANOVA Habitat \times Cage interaction: $F_{(1,16)}=0.70$, $P>0.41$). Hence, the presence of cages did not confound interpretation of the effects of habitat on flow and abrasion. Among clods that were fully caged, loss of

Table 3 Results of ANOVA testing for differences in the percentage cover of morphological groups of algae among habitats (monospecific *E. radiata*, mixed *E. radiata*-Furcals, and gaps), locations and sites on natural reef across South Australia

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
		(a) Encrusting coralline			(b) Articulated coralline		
Habitat	2	104,883.50	39.97	***	27,614.00	6.27	*
Location	3	18,288.15	21.94	***	24,479.60	52.19	***
Site(location)	12	833.71	3.61	***	469.04	2.36	**
Habitat × location	6	2,623.94	5.59	**	4,405.56	35.53	***
Habitat × site(location)	24	469.33	2.03	**	124.00	0.62	ns
Residual	336	230.90			199.15		
		(c) Filamentous turf			(d) Foliose algae		
Habitat	2	12,404.04	9.28	ns	989.14	5.87	*
Location	3	1,387.15	10.03	*	2,154.61	8.86	**
Site(location)	12	138.32	1.53	ns	243.07	2.41	**
Habitat × location	6	1,335.99	6.49	**	168.43	1.29	ns
Habitat × site(location)	24	205.94	2.27	**	131.07	1.30	ns
Residual	336	90.67			100.66		
		(e) Encrusting non-coralline			(f) Juv. canopy-formers		
Habitat	2	371.29	7.00	*	7,142.66	8.87	**
Location	3	408.60	2.90	ns	1,592.47	3.44	ns
Site(location)	12	140.85	5.04	***	462.64	3.92	***
Habitat × location	6	53.01	1.59	ns	805.33	4.67	**
Habitat × site(location)	24	33.31	1.19	ns	172.35	1.46	ns
Residual	336	27.92			118.15		

Data were arcsine(%) transformed. Cochran's *C*-test of homogeneity of variances: $P > 0.05$ for (a), (b), (c), and (f). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns $P > 0.05$. Transformation failed to remove heterogeneous variances for (d) and (e) (Cochran's *C*-test: $P < 0.05$) and significance was judged at the more conservative $\alpha = 0.01$ (Underwood 1997). In such cases, * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$, ns $P > 0.01$

plaster was greatest in gaps but did not differ between mixed and monospecific stands (Fig. 3g, Table 5g). We interpret this as a reduction in water flow beneath canopies relative to gaps. The difference in the loss of plaster between fully caged and uncaged clods was greater in

monospecific than mixed stands (Fig. 3h, Table 5h), suggesting that the intensity of lamina abrasion is greater within monospecific stands. Calculations of the loss of plaster due to abrasion indicated that some loss occurred in gaps (~3%), where abrasion by canopies

Table 4 Natural patterns versus experimental effects among habitats for understory algae

Morphological group	Location	Natural pattern	Experimental effect
Encrusting coralline	Eyre West	G < MX < MO	G < MX < MO
	Eyre East	G < MX < MO	
	Yorke	G < MX < MO	
	Fleurieu	G < MX < MO	
Articulated coralline	Eyre West	G = MX = MO	G > MX = MO
	Eyre East	G > MX = MO	
	Yorke	G > MX > MO	
	Fleurieu	G > MX > MO	
Filamentous turfs	Eyre West	G > MX = MO	G > MX = MO
	Eyre East	G > MX = MO	
	Yorke	G = MX = MO	
	Fleurieu	G > MX = MO	
Foliose algae	Eyre West	G = MX > MO	G > MX = MO
	Eyre East	MX > G = MO	
	Yorke	G = MX > MO	
	Fleurieu	G = MX = MO	
Encrusting non-coralline	Eyre West	MX > G = MO	MX > G = MO
	Eyre East	MX = MO > G	
	Yorke	G = MX = MO	
	Fleurieu	MX > G = MO	
Juv. canopy-formers	Eyre West	G = MX > MO	G = MX = MO
	Eyre East	G > MX > MO	
	Yorke	G = MX > MO	
	Fleurieu	G = MX > MO	

G gap, MX mixed stands, MO monospecific stands

cannot occur. This loss cannot be quantitatively explained in the present study, but may represent effects of drift algae or suspended sediments abrading clods within gaps.

Discussion

One of the most striking and frequently cited patterns from subtidal rocky coasts of the temperate world is that the type and abundance of benthic algae growing beneath subtidal canopies of algae (e.g. kelps) differs greatly from that observed within gaps among canopies (e.g. north-west Atlantic: Chapman and Johnson 1990, Alaska: Dayton 1975, California: Edwards 1998, Australia: Fowler-Walker and Connell 2002). Our observations from South Australia are consistent with this widespread pattern, highlighting associations of understory algae with canopies (e.g. encrusting corallines) or gaps (e.g. articulated corallines and filamentous turfs) that are repeated with great fidelity across > 1,000 km of coastline. Additionally, we observed variation in the structure of understory communities between canopies of different composition (i.e. monospecific vs. mixed). Although ecological differences between monospecific and mixed-species canopies of terrestrial vegetation are well-known (e.g. Cannell et al. 1992), such information is remarkably rare among stands of canopy-forming algae in marine systems. Nevertheless, consistent differences between monospecific and mixed-species canopies of *E. radiata* suggest that partitioning observations between these two types of habitat could enhance precision in a system where enormous spatial variability is often emphasised (e.g. Wernberg et al. 2003), and could therefore generate greater power for predictive models (Peters 1991).

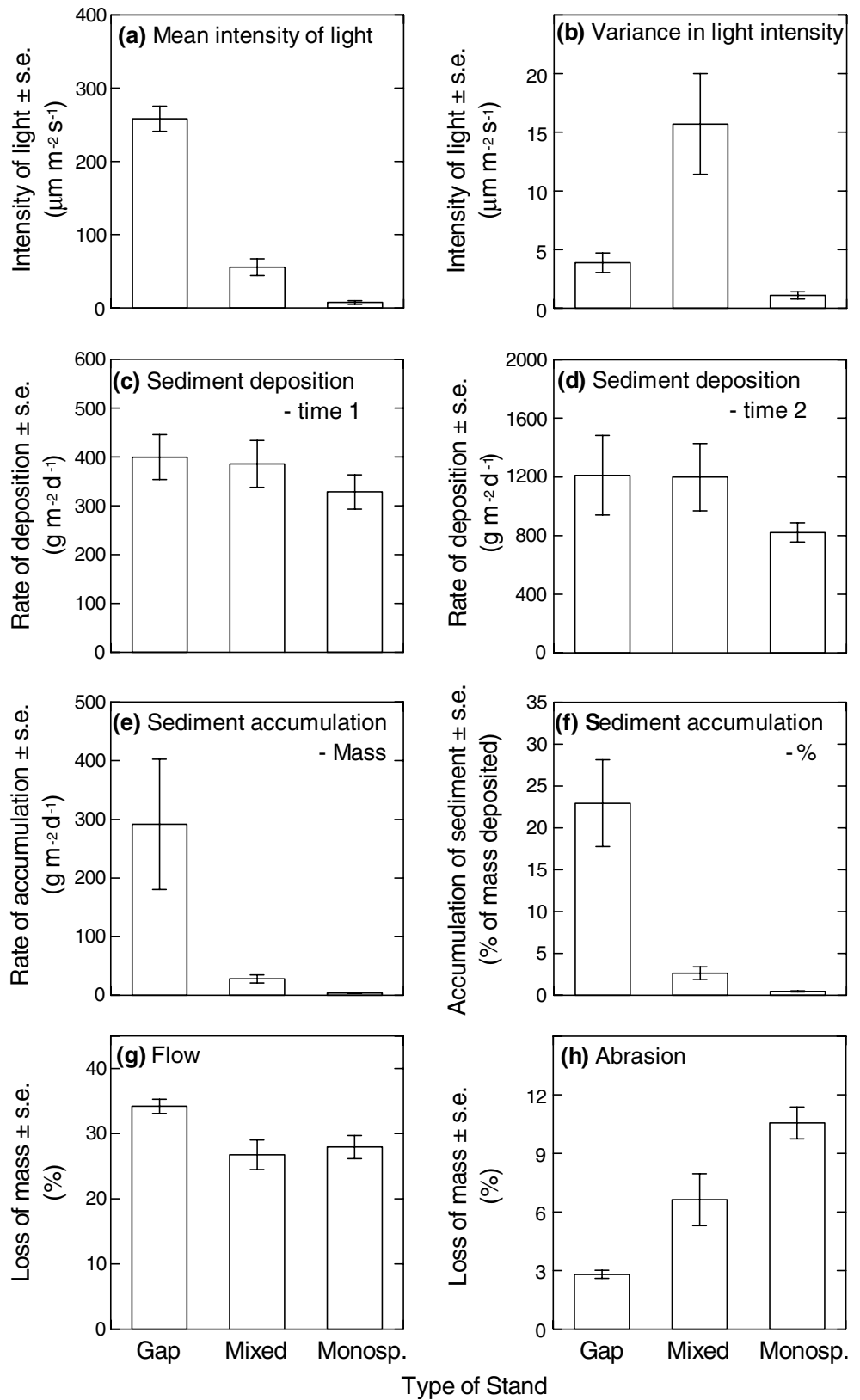
Manipulating the presence and composition of canopies (monospecific *E. radiata* vs. mixed *E. radiata*-Fucales vs. gaps) demonstrated that we could recreate natural patterns of understory structure using experimental protocols. Such consistencies illustrate how the presence and composition of canopies can act as a filter to limit which subsets of species from the locally available pool are able to coexist with canopies (monospecific or mixed). The presence of canopies enhanced the abundance of encrusting corallines, with greater covers observed beneath monospecific relative to mixed-species canopies. Additionally, mixed-species canopies typically supported greater covers of encrusting non-coralline algae than either monospecific canopies or gaps. Both articulated corallines and filamentous turfs were more extensive in gaps than beneath canopies, although mixed-species canopies often supported greater covers of articulated corallines relative to monospecific canopies on natural reef, but not on experimental reefs. Considerable spatial variability in the abundance of foliose algae among habitats may be attributable to the large number of species (mainly Rhodophytes and Chlorophytes) included in this group. Species of Rhodophyta

and Chlorophyta can vary greatly in their resource requirements (e.g. differing demands for light: Gómez et al. 2004), and therefore it is perhaps not surprising that foliose algae exhibited no clear association with one type of habitat over another. Juvenile canopy-formers were typically most abundant within gaps and beneath mixed-canopies on natural reef, but poor recruitment to all experimental reefs precluded a meaningful comparison between natural and experimental results. Such inconsistencies may be due to a probable difference in the ages of experimental (~1 year) and natural communities (> 1 year), whereby insufficient time was allowed for the recruitment and growth of some types of algae on experimental reefs. Importantly, while some inconsistencies were observed, key patterns frequently emerged that were consistent between natural and experimental reefs.

Consistencies between natural patterns and experimental effects provide a foundation for proposing assembly rules for understory algae. The general pattern emerging from this research is that the subsets of species that assemble to subtidal rocky substrata in South Australia are predictable given knowledge of the presence and composition of canopies incorporating *E. radiata*. Specifically, we propose the following assembly rule: subtidal assemblages of understory algae on exposed rocky coasts of mainland South Australia (i.e. Irving et al. 2004b) will be (1) monopolised by encrusting coralline algae where canopies of *E. radiata* occur as a monospecific stand, (2) comprised of encrusting corallines, encrusting non-corallines, and sparse covers of articulated corallines, where canopies of *E. radiata* are mixed with Fucales (i.e. *Cystophora* spp., *Sargassum* spp.), and (3) comprised of extensive covers of articulated corallines and filamentous turfs, as well as sparse covers of foliose algae and juvenile canopy-formers, where canopies are absent (i.e. within gaps). It is necessary to test the utility of this rule as a general predictor of ecological pattern. In other words, does this rule apply to all subtidal coasts supporting *E. radiata*? Spatial variability in canopy-understorey associations among biogeographic regions (e.g. southern vs. eastern Australia: Irving et al. 2004b), and even within regions (e.g. Fig. 2, Table 4) suggests limits to the generality of this rule. Even so, we wish to emphasize the worth of proposing such rules for providing a testable framework that may increase our predictive understanding of how understory communities assemble on rocky coasts.

The predictive power of assembly rules is likely to be enhanced where they include knowledge of the specific mechanisms driving the assembly of communities (see review in Belyea and Lancaster 1999). Modification of the physical environment by canopies of algae appears key to explaining observed differences in the assembly of understory (i.e. “rule” 9 of Table 1 in Belyea and Lancaster 1999). Monospecific and mixed-species canopies of *E. radiata* greatly reduced the intensity of light reaching the understory. Such conditions favour the growth of encrusting corallines (Figueiredo et al. 2000;

Fig. 3 Differences in environmental variables among gaps, mixed stands, and monospecific stands of *E. radiata*



Irving et al. 2004a), but appear to inhibit the growth of articulated corallines and filamentous turfs (Kennelly 1989; Connell 2005). Greatest variability in the intensity

of light was observed beneath mixed-species canopies, which may contribute towards enhanced growth and survival of articulated corallines and foliose algae be-

Table 5 Results of ANOVA ($F_{(2,12)}$ for all variables) testing for differences in the physical conditions among habitats, with associated SNK tests identifying the location of detected differences

Variable	<i>F</i>	<i>P</i>	SNK tests
(a) Mean light intensity	123.80	***	G > MX > MO
(b) Variation in light intensity	25.57	***	MX > G > MO
(c) Sediment deposition—time 1	0.76	ns	G = MX = MO
(d) Sediment deposition—time 2	1.13	ns	G = MX = MO
(e) Sediment accumulation—mass	58.07	***	G > MX > MO
(f) Sediment accumulation—% of deposition	49.48	***	G > MX > MO
(g) Flow	4.97	*	G > MX = MO
(h) Abrasion	18.10	***	G < MX < MO

Data were arcsine(%) transformed for (f), (g) and (h). $\ln(x+1)$ transformation for (b) and (e) was needed to meet the assumption of homogeneity of variances (Cochran's *C*-test: $P > 0.05$ for all variables)

G gap, *MX* mixed stands, *MO* monospecific stands

* $P < 0.05$, *** $P < 0.001$, ns $P > 0.05$

neath mixed canopies relative to monospecific canopies. The rate of sediment deposition was similar among the three habitats, although the amount of sediment that accumulated on understorey boulders was greatly reduced beneath canopies. The combination of enhanced light and sedimentation conditions (i.e. within gaps) is known to facilitate greater covers of erect species of algae that trap sediments into their structure (i.e. turf-forming and articulated coralline algae), whereas reduced light and sediment accumulation (i.e. beneath canopies) facilitates greater covers of encrusting coralline algae (Connell 2005).

Water flow was slightly greater in gaps than beneath canopies, which is consistent with observations from other forests of algae (Jackson and Winant 1983; Duggins and Eckman 1994). Little information is available on the effects of variable water flow on understorey algae, but reduced amounts of flow may contribute toward differences in the assembly of understorey by affecting the dispersal and delivery of spores to colonisable substrata (Santelices 1990). Abrasion of the understorey by the lamina of canopy-formers is known to have negative effects on the abundance of articulated corallines and filamentous turfs (Cheroske et al. 2000; Irving and Connell, *Mar Ecol Prog Ser*, in review). We observed that the intensity of abrasion was greater beneath monospecific than mixed-species canopies, which may contribute toward an explanation of why greater covers of articulated corallines are often observed beneath mixed-species canopies. In sum, it appears that canopies of *E. radiata* can strongly modify physical conditions to create heterogeneous but largely predictable patterns in the assembly and maintenance of understorey (Connell 2005).

Spatial consistency of pattern gives weight to arguments that it may be possible to scale-up knowledge from smaller to larger scales (Thrush et al. 1997) and increase our predictive understanding of natural systems. Encrusting corallines, articulated corallines and filamentous turfs characterise much of the benthic habitat across temperate Australia (Underwood et al. 1991; Irving et al. 2004b), and differences in their covers among habitats were largely consistent from site to site in South

Australia. As such, constraints imposed by canopies on the assembly of these understorey taxa to rocky substrata appear predictable from local scales (i.e. within a site) to larger scales (i.e. among sites and locations) on comparable coastlines. In contrast, differences in the covers of other groups (e.g. foliose algae) among habitats were variable among sites and locations, suggesting poor predictability of their association with canopy-formers.

Generalities in ecology may present themselves as broadly repeatable patterns and responses in nature (Lawton 1999; Fowler-Walker and Connell 2002). Similar to stands of marine algae, the type and abundance of understorey vegetation within stands of terrestrial canopy-formers often differs greatly to that occupying gaps (Grime 1979; Callaway 1995). For decades, studies of succession in terrestrial forests have typically shown large increases in the abundance of fast-growing, opportunistic, and shade-intolerant species following the loss of canopies (e.g. grasses and herbs in beech-hemlock forest: Peterson and Pickett 1995, oak woodlands: McPherson and Weltzin 1998; also see Grime 1979; West et al. 1981). Greater covers of opportunistic species following canopy-loss are also observed among stands of freshwater (e.g. reed marsh: Lenssen et al. 1999) and marine vegetation (e.g. kelp forests: Dayton 1975; Edwards 1998), suggesting generality in the functional responses of understorey to canopy-loss across widely differing environments. It would be valuable to know whether the processes driving such responses are similar among systems. For example, canopies typically reduce the intensity of light and understorey taxa often respond predictably (positively or negatively) to such changes in the light environment (e.g. tropical forests: Watling and Press 2000, marine forests: Irving et al. 2004a). We acknowledge that differences in the extent of a canopy, its composition, and so on will modify the influence of light, but we wish to emphasise that there is potential for tests of generalities in the effects of canopies on the assembly of understorey communities within relatively similar environments (e.g. tropical vs. temperate rain forest) and between widely different environments (e.g. oak woodlands vs. kelp forests).

In conclusion, contemporary ecology is shifting towards a more sophisticated understanding of the environmental factors that cause pattern in nature (Keddy 1999). To this end, the concept of assembly rules enables us to propose testable predictions about the structure of communities based on defined features of the environment. We propose that the structures of subtidal understorey communities of algae in South Australia may be predicted from knowledge of the presence and composition of canopies incorporating *E. radiata*. Testing whether this prediction can be generalized to other coastlines supporting *E. radiata*, or even to canopies formed by species other than *E. radiata*, would provide an indication of its spatial and taxonomic limitations. Regardless of the results of such tests, we emphasise the potential of assembly rules as a useful tool for increasing our predictive understanding of the organisation of understorey communities beneath subtidal canopies of marine algae. Indeed, where knowledge of generality and predictability in ecology is embraced (Peters 1991), assembly rules show great promise for progressive outcomes.

Acknowledgments P. Keddy, L. Benedetti-Cecchi, and J. Estes gave insightful suggestions on this manuscript and their advice and encouragement were greatly appreciated. We also thank C. Körner and three anonymous reviewers for their useful and constructive comments. We thank M. Anderson for an advance copy of her PERMANOVA software, and T. Elsdon, B. Russell, J. Stehbens, A. Bloomfield, T. Greig, and C. Pale for field support. This research was supported by grants from the Australia and Pacific Science Foundation and the Nature Foundation of South Australia to A.D.I and S.D.C., and an Australian Research Council Discovery grant to S.D.C. The research in this manuscript complies with the current laws of Australia.

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