

Biogeographical variation in brown algal polyphenolics and other secondary metabolites: comparison between temperate Australasia and North America

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Summary. Polyphloroglucinol phenolics are the best known example of chemical deterrents against herbivores in temperate marine systems. However, most of the research on these compounds has been done in North America, where phenolic levels in algae are often low. I show here that algae in the Orders Fucales and Laminariales in temperate Australia and New Zealand typically contain very high levels of polyphenolics – much higher than species in these orders in North America. The median value for the distribution of mean phenolic levels for 25 North American species is 1.33% total phenolics (dry wt.); for 37 Australasian species, the median is 6.20%. Significant spatial, temporal, and intraplant variation in phenolic content occurs in a number of species in Australasia, but this does not significantly alter my major conclusion. Phenolic levels in drift algae (an important food source for some herbivores) detached for up to two weeks are also not significantly different from living, attached plants. Many species in the Fucales in Australasia also contain non-polyphenolic secondary metabolites that are not found in North American species. Thus herbivores in Australasia face greater amounts, and a greater range, of putative chemical defenses in brown algae than do herbivores in similar systems in North America. Any general theory for the evolution of marine plant/herbivore interactions must take into account such broad-scale biogeographical (and taxonomic) patterns.

Key words: Brown algae – Polyphenolics – Chemical defenses – Herbivory – Biogeography

Herbivores in marine benthic communities can have dramatic effects on populations and communities of benthic macroalgae (Lawrence 1975; Lubchenco and Gaines 1981; Hawkins and Hartnoll 1983). An important way in which the algae can minimize the effects of the herbivores is via the production of chemical defenses (Steinberg 1984, 1985, 1988; Paul 1987; Paul and Fenical 1986; Hay et al. 1987a, b).

The best known examples of algal chemical defenses in temperate marine systems are studies of the effects that brown algal (Division Phaeophyta) polyphenolic (polyphloroglucinol) compounds have on invertebrate herbivores (Geiselman and McConnell 1981; Anderson and Velimirov 1982; Steinberg 1984, 1985, 1988; Johnson and Mann 1986; van Alstyne 1988). Polyphloroglucinols are ubiquitous in

brown algae (reviewed by Ragan and Glombitza 1986) and can have a wide variety of effects against both herbivores, and other natural enemies of brown algae (Conover and Sieburth 1964).

Most studies on the interaction between algal polyphenols and marine herbivores have been done in North America (Geiselman and McConnell 1981; Steinberg 1984, 1985, 1988; Johnson and Mann 1986; van Alstyne 1988) on species from two orders of phaeophytes, the Laminariales (kelps) and the Fucales. This work suggests two general conclusions. First, different species, plants within a species, or parts of a single plant vary considerably in levels of polyphenolics produced. However, many of the most abundant species of brown algae in North America contain quite low levels of polyphenolics (e.g. – 0–2% by dry wt.; Steinberg 1985). Secondly, common generalist herbivores are consistently deterred by plant tissue that is high in polyphenolics (Steinberg 1984, 1985; Johnson and Mann 1986), and are deterred by polyphenolics in direct experimental tests (Geiselman and McConnell 1981; Steinberg 1988).

Brown algae (Dayton 1985; Schiel and Foster 1986) and herbivores (Dakin 1980; Stephenson and Stephenson 1972) similar to those in North America are abundant on most temperate rocky shores. However, interactions between marine herbivores and algal polyphenolics in other parts of the world may be different. Estes and Steinberg (1988) argued that the intensity of sublittoral plant/herbivore interactions in North America has been relatively weak in the recent past, due largely to the influence of sea otters as predators on the herbivores. They suggested that marine herbivores in other temperate regions of the world were not preyed on as heavily, and may have had a greater effect on the algae, and on the evolution of algal defensive compounds. In particular, Estes and Steinberg (1988) predicted that in temperate New Zealand and Australia: 1) Levels of polyphenolics in brown algae would on average be much higher than those in related North American species, and: 2) Common generalist herbivores, having evolved in the presence of a phenolic-rich flora, would have evolved greater tolerance to polyphenolics than have similar herbivores in North America.

The purpose of this paper is to begin to test the predictions of Estes and Steinberg (1988). I describe phenolic levels in common species of brown algae in the Fucales and Laminariales at various sites in temperate New Zealand and Australia, and argue that levels of polyphenolics in Australasian algae are typically much higher than those

in North America. Moreover, the Australasian species contain other, non-polyphenolic compounds, not found in North American kelps or furoids. Common brown algae in temperate Australasia are in general much richer in potential chemical defenses than are similar algae in North America.

Materials and methods

Description of algae and sites

All the algae analyzed in this paper are brown macroalgae (Phaeophyta) belonging to two orders, the Laminariales (true kelps) and Fucales (furoids).

As in North America (and most temperate rocky shorelines), these two orders make up the dominant fraction of algal biomass along rocky coasts in temperate Australasia (Choat and Schiel 1982; Womersley 1981a, b; Kirkman 1984). There are differences between the two geographical regions, however. First, kelps and furoids are largely restricted to the sublittoral in temperate Australasia, with a few exceptions (e.g., *Hormosira banksii* and *Durvillaea potatorum*; Dakin 1980; Womersley 1981b). This is unlike North America, where kelps (*Egregia menziesii*) and furoids (*Fucus*, *Ascophyllum*, etc.) are also abundant in the littoral zone (Lamb and Zimmerman 1964; Ricketts et al. 1968). Secondly, there are differences in relative diversity among the two regions. The diversity of true kelps in temperate

Australasia is much less than in the northeast Pacific (Lindauer et al. 1961; Druehl 1970; Womersley 1967; Estes and Steinberg 1988), and most kelps in Australasia have relatively restricted distributions. An exception to the latter point is *Ecklonia radiata*, which is probably the most abundant (cover and biomass) alga in temperate Australasia (Kirkman 1984).

The Fucales differ as well. The family Fucales, diverse and abundant in the intertidal in North America (Lamb and Zimmerman 1964; Ricketts et al. 1968), is represented in Australasia only by the genus *Xiphophora* (Womersley 1967). Conversely, the families Cystoseiraceae and Sargassaceae are much more diverse and abundant in Australasia (Nizammudin 1970; Womersley 1967, 1981b).

Algae were collected at several sites in New South Wales and South Australia, and at one site each in Victoria and New Zealand (Fig. 1). Collections in New Zealand were made along approximately 2 kilometers of coast within the Marine Reserve adjacent to the Leigh Marine Laboratory of the University of Auckland, described by Ayling (1981), Choat and Schiel (1982), and Andrew and Stocker (1982). Description of sites in New South Wales are in Underwood et al. (1985), Fletcher (1987), and Kennelly (1987). West Island (South Australia) is described in Shepherd and Womersley (1970). Other sites in South Australia varied from moderately exposed, high relief rock outcrops (Pinnacle Beach), to more protected, subtidal rock benches (Edithburgh). Kelps and/or furoids were abundant at all sites.

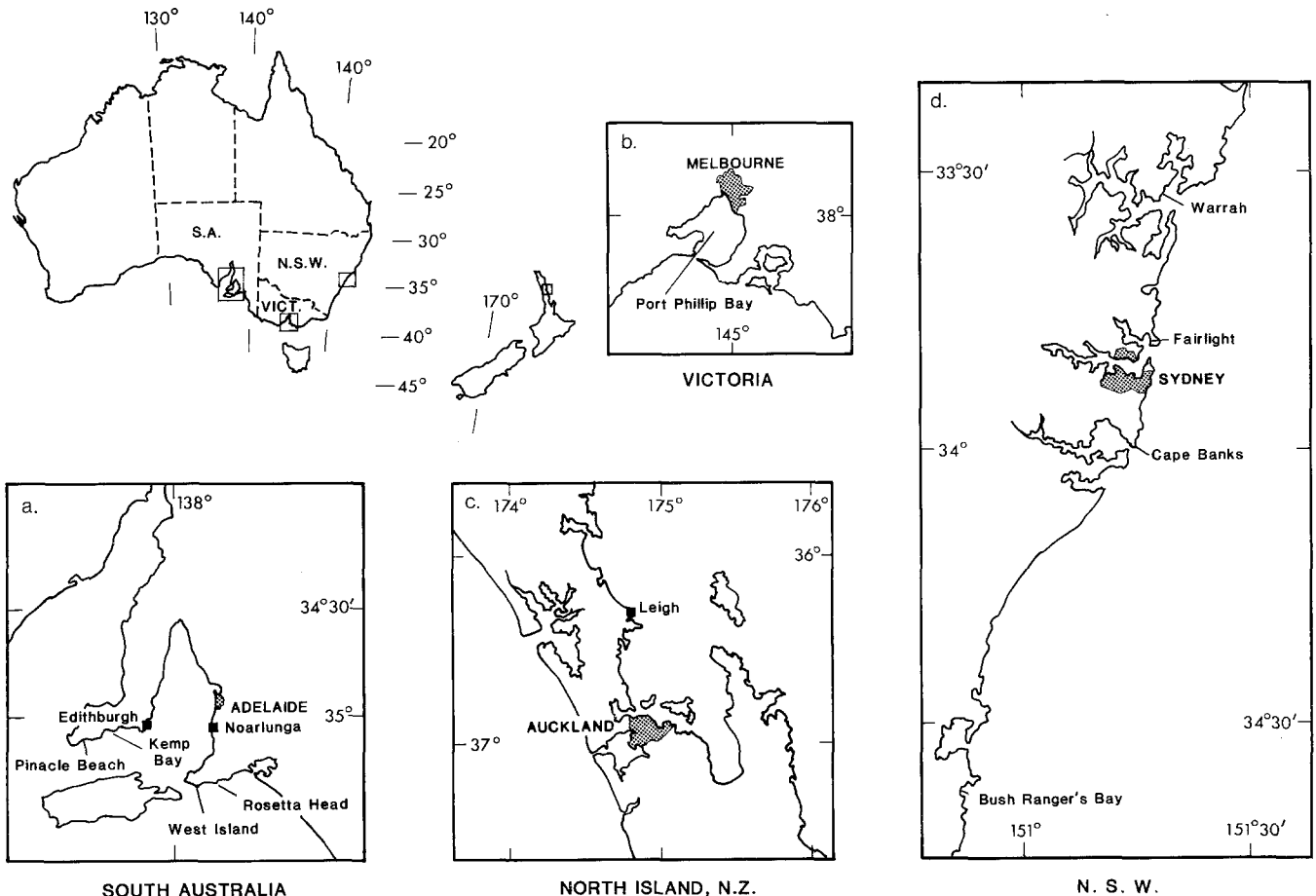


Fig. 1a-d. Map of sites where algae was collected in New Zealand and Australia

I attempted to collect and analyze all species of fucoids and kelps at each site (as determined by observation or species lists). This was largely successful in New Zealand and New South Wales. In South Australia, because a larger number of sites was examined, and the diversity of fucoids is quite high (e.g., Shepherd and Womersley 1970), analyses were sometimes restricted to the visually abundant species. Samples from Victoria were restricted to *Macrocystis angustifolia* and *Durvillaea potatorum*.

Chemical methods

Chemical analyses of all algae, except *M. angustifolia* and *D. potatorum*, were begun within several hours of collection. On hot days, or where field sites were far from the laboratory, algae were kept cool on ice in transit. *M. angustifolia* and *D. potatorum* were collected in Victoria, frozen, and analyzed in Sydney.

Algal samples were homogenized and extracted in aqueous methanol (Ragan and Jensen 1977; Steinberg 1985). Generally cross sections of the thallus of the algae, including main axes and smaller secondary parts (blades, leaflets, ramuli, etc. [Bold and Wynne 1981]) were used in the analyses. Exceptions to this included *Macrocystis angustifolia* and *Lessonia variegata*, where only blades were assayed, and selected other species where intraplant variability was explicitly examined (Results). Total phenolic content of the algae was measured by the Folin-Denis technique, which has been used extensively to assay phenolic levels in both marine algae (Ragan and Jensen 1977; Geiselman 1980; Steinberg 1985; Johnson and Mann 1986) and terrestrial plants (Swain and Hillis 1959). Phloroglucinol was used as a standard (Ragan and Jensen 1977).

As discussed by Ragan and Jensen (1977) and Steinberg (1985), there are potential difficulties in comparing phenolic levels among many species of algae via colorimetric assays such as the Folin-Denis technique. Differences in the extractability of different phenolics, or their reactivity to the assay reagents, will temper the conclusions drawn from such surveys. However, the reactivities of a wide range of algal phenolics to the Folin-Denis assay are similar. For example, the reactivity in this assay of purified polyphenolics from 5 species of algae (including *Ecklonia radiata* and *Sargassum vestitum* from Australia) and phloroglucinol differ by less than 25% (Steinberg 1988, and unpublished work). The reactivities of an additional 11 of 12 polyphenolics of known polymer type from a diversity of algae differ by less than a factor of two (Ragan and Glombitza 1986). Thus large differences (perhaps greater than a factor of ca. 1.5) in Folin-Denis phenolics among species should reflect real differences in the levels of phenolic compounds in the plants. There is also no reason to expect that there should be an overall bias in the reactivities of phenolics from Australian vs. North American plants.

Analysis of phenolic content of "drift algae"

As well as consuming living, attached plants, many marine herbivores (including Australasian ones) consume benthic macroalgae after they become detached from the substratum and form drift (Harrold and Reed 1986; Andrew and Stocker 1987). Thus changes in the levels of phenolics in drift algae have considerable relevance for the effects of these compounds on marine herbivores.

Changes in phenolic levels in "drift" algae were measured in two experiments at Cape Banks (N.S.W.) with the kelp *Ecklonia radiata* and the fucoid *Sargassum vestitum*. In the first experiment, done in August of 1985, 4 whole plants of each species were detached from the substratum and placed in galvanized steel cages at a depth of 5 m. Samples of each plant were taken daily over 3 days and total phenolic levels measured. In the second experiment, done in Jan./Feb. of 1988, 15 plants of each species were detached. Ten plants of *Sargassum vestitum* were placed in 20 l plastic bins covered with plastic mesh at a depth of 4 m. Ten *E. radiata* were tethered to these bins with 0.5 m lengths of insulated electrical wire. The 5 remaining plants of each species were collected and their phenolic content analyzed (day "0" samples), and after 7 and 14 days five plants of each species were collected and assayed for phenolics.

Statistical analyses

T-tests, and ANOVA's (as appropriate depending on the number of treatment groups in an analysis), were used to examine intraplant and intraspecific variation in phenolic content among the algae. Because of the breadth of geographical localities studied, collection of the algae in different places (sites or regions) was often done in different seasons or years. Thus analyses of a given species have generally been broken up into several single-factor analyses for spatial, temporal, or intraplant variation, rather than considering all these factors within a single multifactorial analysis. Details of the analyses are described in the Results section. Homogeneity of variances was examined in each case using an *F*-max, Cochran's, or Bartlett's tests for *t*-tests, balanced, and unbalanced ANOVA's respectively. In instances where treatment groups were heteroscedastic, the data were transformed by $\ln(x)$.

Results

Overall levels of polyphenolics; comparison to the northeast Pacific

The total phenolic content of the 37 species of Australasian fucoids and kelps analyzed in this study are on average much higher than species from the northeast Pacific analyzed by the same methods (Table 1, Fig. 2; Steinberg 1984, 1985). More than half (14) of the species from the northeast Pacific contain levels below 2% by dry weight; only 3 species (8%) from Australasia contain such low levels (including the only two species from Victoria, *Macrocystis angustifolia* and *Durvillaea potatorum*, where the fewest samples were collected). Only one species, *Halidrys dioica* (Steinberg 1985) from the northeastern Pacific contained greater than 6% mean total phenolics. Half (19) of the Australasian species contained these levels. Greater than 20% of the Australasian species contained 10% or more total phenolics. The medians of the distribution of mean phenolic levels for the northeast Pacific and Australasia are 1.33% and 6.20%, respectively. Algal total phenolic levels are highly significantly different between the two regions, as determined by a Wilcoxon's rank sum test comparing the mean level of phenolics of species from Australasia to those from the Northeast Pacific ($t = 4.53$, $P \leq 0.001$). A similar analysis

Table 1. Mean total phenolic content of species of Laminariales and Fucales from northern New Zealand, and southeastern Australia. Data are averaged across different sites within a region. Data are $x \pm S.E.$ expressed as percent phenolics by dry weight. Differences in phenolic levels within species but between years or seasons were tested by t -tests or single-factor ANOVA's

New Zealand	Signif.	<i>N</i>	Spring 1984	<i>N</i>	Late Winter 1986		
<i>Carpophyllum maschalocarpum</i>							
entire thallus		8	10.37+0.58	5	11.33+0.68		
vegetative thallus		2	11.34+1.79				
receptacles		2	6.19+0.03				
<i>C. angustifolium</i>	**	8	10.14+0.69	7	13.66+0.92		
<i>C. plumosum</i>	*	8	9.80+0.31	8	7.68+0.73		
<i>C. flexuosum</i>				6	9.34+0.64		
<i>Sargassum sinclairii</i>		8	11.58+0.37	6	10.18+0.89		
<i>Ecklonia radiata</i> (adult 2° lam.)	*	19	9.28+0.44	16	11.19+0.71		
<i>Cystophora torulosa</i>		7	4.93+0.23	6	5.26+0.47		
<i>Landsburgia quercifolia</i>		8	4.29+0.44	6	5.01+0.47		
<i>Xiphophora chondrophylla</i>	*	8	3.18+0.17	6	2.18+0.26		
<i>Hormosira banksii</i>		5	3.75+0.17				
<i>Lessonia variegata</i>		6	1.30+0.27				
New South Wales	Signif.	<i>N</i>	Summer 1984–1985	<i>N</i>	Winter 1985	<i>N</i>	Winter 1987
<i>Ecklonia radiata</i>		19	5.48+0.56	5	5.63+0.90	9	6.04+0.91
<i>Sargassum vestitum</i>		17	6.71+0.42	6	6.97+0.58	9	6.40+0.43
<i>S. linearifolium</i>	***	15	4.02+0.28	7	1.00+0.12	5	0.90+0.16
<i>S. globulariaefolium</i>	**			6	7.85+0.67	5	4.52+0.46
<i>Sargassum</i> sp. 1		7	3.00+0.37				
<i>Sargassum</i> sp. 5		4	3.18+0.33				
<i>Cystophora moniliformis</i>		11	9.21+0.60				
<i>Phyllospora comosa</i>		19	2.67+0.48				
<i>Acrocarpia paniculata</i>		7	5.16+0.91				
<i>Hormosira banksii</i>		7	3.47+0.49				
South Australia		<i>N</i>	Summer 1984–1985	<i>N</i>	Winter 1985		
<i>Ecklonia radiata</i>		14	7.46+0.86				
<i>Cystophora moniliformis</i>		6	12.16+1.01				
<i>C. subfarinata</i>							
whole thallus		12	12.16+0.62				
axis		4	13.96+1.52				
laterals		4	13.49+0.66				
<i>C. expansa</i>		6	8.87+1.17				
<i>C. polycistidea</i>		9	6.66+0.77				
<i>C. brownii</i>		4	13.02+0.56				
<i>C. platylobium</i>		3	4.46+1.43				
<i>C. monilifera</i>		9	7.63+0.75				
<i>C. siliquosa</i>		7	13.10+0.64				
<i>Caulocystis cephalornithos</i>		7	4.42+0.39				
<i>Sargassum bracteolosum</i>		8	11.46+0.99				
<i>S. decipiens</i>		6	5.18+0.20				
<i>Sarg.</i> sp. 3 (<i>linearifolium</i> ?)		6	6.92+0.38				
<i>Sargassum</i> sp. 2		6	4.24+0.55				
<i>Sargassum</i> sp. 4		3	4.46+0.49				
<i>Scaberia agardhii</i>		6	7.25+0.87				
<i>Seirococcus axillaris</i>		5	4.64+0.54				
<i>Scytothalia dorycarpa</i>		6	6.01+0.71				
Victoria							
<i>Macrocystis angustifolia</i>				6	0.62+0.08		
<i>Durvillaea potatorum</i>				5	0.63+0.12		

Significances given as * ($P < 0.05$), ** ($P < 0.01$), or *** ($P < 0.001$)

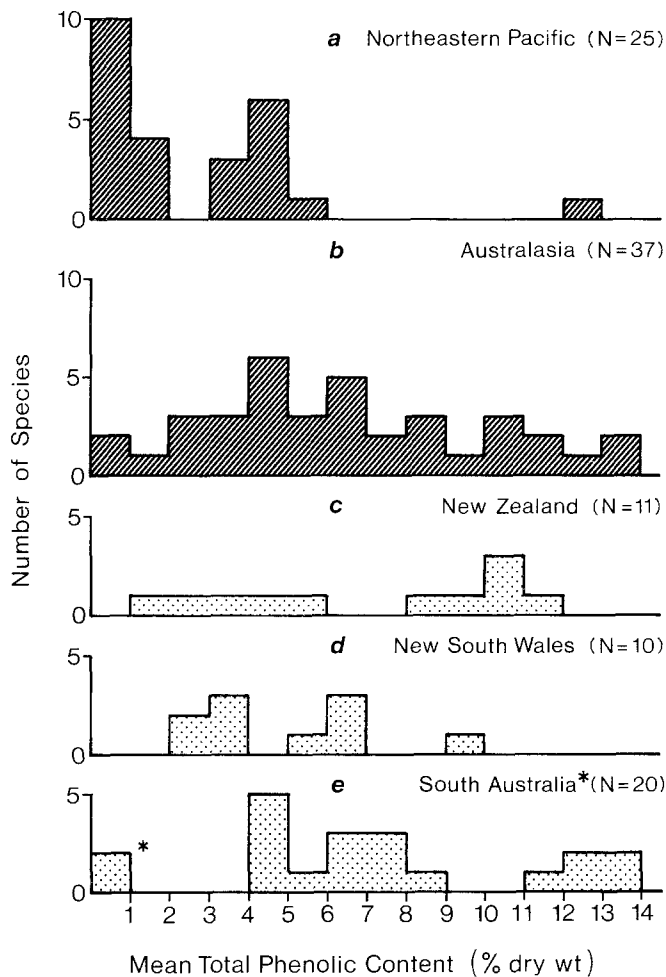


Fig. 2a-e. Phenolic content of furoid and laminarian algae from the temperate northeastern Pacific (Steinberg 1984, 1985) and temperate Australasia (summarized from Table 1). Species analyzed from the northeastern Pacific collected from S. California to Alaska (Steinberg 1984, 1985). Number of species assayed (N) in parentheses. Numbers of species assayed in N.Z., N.S.W., and S. Austr. do not sum to Australasian totals because some species occur within more than one area in Australasia. In such cases the mean averaged across all areas is given in 2b. Two species from Victoria are included in the South Australian data e, and are denoted by *

(Kruskal-Wallis test) revealed no significant variation among areas within Australasia ($H=4.45$, $P>0.1$).

Variation in phenolic levels showed some taxonomic patterns. Levels in 2 of the 3 kelps analyzed (*Macrocystis angustifolia* and *Lessonia variegata*) were quite low, comparable to typical levels found in kelps in the northeast Pacific (Steinberg 1985). However, the 2° laminae (which comprise most of the biomass of the plant) of the third, most common species of kelp, *Ecklonia radiata*, were consistently rich in phenolics. Two common genera of furoids that are endemic to Australasia, *Carpophyllum* and *Cystophora*, also contained high levels of phenolics. *Sargassum*, another diverse and abundant genus in Australasia, was typically phenolic-rich, but quite variable between, and in some cases (*S. linearifolium*) within, species (Table 1).

Spatial, temporal, and intraplant variation in phenolic levels

Biogeographical patterns are confounded if local variation within a region is as great as that between regions (Ortega 1986). To insure that the overall patterns described above were consistent in space and time, I measured intraspecific or intraplant variation in a number of Australasian brown algae.

Significant intraspecific variation in phenolic content occurred in a number of species. Year to year differences were observed in *Carpophyllum angustifolium*, *C. plumosum*, *Xiphophora chondrophylla*, and *Ecklonia radiata* from New Zealand, and *Sargassum globulariaefolium* from New South Wales (Table 1). Phenolic levels in *Sargassum linearifolium* from New South varied with season, reaching their lowest levels in winter (Table 1; Steinberg, unpublished work).

Significant variation in phenolic content among sites was observed in *Phyllospora comosa* from New South Wales, and in *Cystophora expansa* and *Sargassum* sp. 2 from South Australia (Table 2). Spatial variation in phenolics in *Cystophora moniliformis* and *Ecklonia radiata*, which were both collected in at least two areas and several sites, was analyzed by comparing among all sites (independent of area) via single-factor ANOVA. Spatial variation in both *C. moniliformis* ($F_{3,16}=12.37$, $P<0.001$) and *E. radiata* ($F_{6,43}=7.17$, $P<0.001$) was highly significant. The pattern of variation among sites for *C. moniliformis*, as determined by SNK tests ($\alpha=0.05$), was Edithburgh (S.A.) > Kemp Bay (S.A.) > Fairlight (N.S.W.) = Rose Harbor (S.A.). SNK tests for *E. radiata* indicated that plants from New Zealand were higher in phenolic content than plants from all sites in Australia except those from Noarlunga Reef in S. Australia. No sites within Australia were significantly different from one another. Phenolic levels in *E. radiata* in New Zealand did not vary significantly with depth (Table 3; $t=0.31$, $df=17$, $P>0.5$).

Intraplant variation in phenolics was investigated in three species, most intensively for *Ecklonia radiata*. Numbers of samples and types of tissues analyzed differed among the different regions (Table 3), but several results are clear. In New Zealand (Table 3), stipes (see Kirkman 1984, Fig. 3) are significantly lower in phenolic content than secondary laminae (t -test, $t=11.04$, $df=10$, $P<0.001$). In New South Wales (Cape Banks; Table 3), stipes, primary laminae, and secondary laminae from 4 plants were compared using a single-factor ANOVA followed by SNK tests with $\alpha=0.05$ ($F_{2,9}=23.73$, $P<0.001$. Secondary laminae > primary laminae = stipes). Sori, the reproductive tissues of *E. radiata* which are borne as patches on the secondary laminae, do not differ in phenolic content from the vegetative tissue of the secondary laminae (Table 3; Single-factor ANOVA, $F_{2,12}=0.23$, $P<0.5$).

The phenolic content of *Ecklonia radiata* also varies with age. Juvenile plants (plants with a single blade less than 15 cm in length) at Cape Banks (N.S.W.) contain higher levels of phenolics than do adult secondary laminae in both summer and winter (Table 3). This result was determined by an unbalanced Model I two-factor ANOVA (plant age X season) in which the only significant F value was for the effect of plant age ($F_{1,24}=5.95$, $P<0.025$).

The thin laterals of *Cystophora subfarinata* (Womersley 1964) are not significantly different in phenolic content from the central straplike axis (Table 1; t -test, $t=0.30$, $P>$

Table 2. Variation in total phenolic content (as % dry wt.) of brown algal species from different sites in New South Wales and South Australia. Data from New South Wales are from Summer, 1984–1985. South Australia data from Winter 1985. Data are $\bar{x} \pm 1$ S.E. Sample sizes in parentheses. Only sites in which sample sizes were ≥ 3 are presented

Species	Signif.	New South Wales					
		Cape Banks	Fairlight	Bush Rangers Bay	Warrah		
<i>Ecklonia radiata</i>							
adult 2° laminae		6.77+0.90 (9)	4.56+0.56 (6)	3.98+0.95 (4)			
juveniles		8.87+1.07 (10)		5.34+0.31 (4)			
<i>Sargassum vestitum</i>		6.91+0.42 (14)	5.79+0.24 (6)	8.27+1.50 (3)			
<i>S. linearifolium</i>		3.77+0.38 (9)		4.64+0.55 (5)			
<i>Phyllospora comosa</i>	**			4.20+0.57 (10)	0.97+0.72 (9)		
<i>Hormosira banksii</i>		4.24+0.35 (3)	3.01+0.36 (4)				
		South Australia					
		Edithburg	Rosetta Head	Kemp Bay	Pinnacle Beach	W. Island	Noarlunga Reef
<i>Ecklonia radiata</i>			5.01+0.43 (3)		6.56+1.06 (4)		7.52+1.09 (5)
<i>Cystophora moniliformis</i>	**	15.65+1.12 (3)	8.42+0.81 (3)	12.43+0.57 (3)			
<i>C. subfarcinata</i>		13.61+1.33 (3)	13.11+1.67 (3)	12.84+1.28 (3)	12.54+1.51 (3)		
<i>C. expansa</i>	*		6.58+1.28 (3)	11.17+0.99 (3)			
<i>C. polycystidea</i>		5.40+0.31 (6)			9.17+1.40 (3)		
<i>C. monilifera</i>			9.72+1.61 (3)			6.59+0.59 (6)	
<i>C. siliquosa</i>				13.86+1.06 (3)	12.53+0.79 (4)		
<i>Caulocystis cephalornithos</i>		4.16+0.26 (3)			4.80+0.93 (3)		
<i>Sargassum bracteolosum</i>			9.60+0.79 (3)		11.35+1.41 (3)		
<i>Sargassum</i> sp. 2	**	5.39+0.20 (3)			3.10+0.40 (3)		

Asterisks indicate significant variation in phenolic levels among sites at $P < 0.05$ (*), $P < 0.01$ (**), or $P < 0.001$ (***) as determined by t -tests or single-factor ANOVA's

Table 3. Intraspecific and intraplant variation in phenolic content in the kelp *Ecklonia radiata*. Data for New Zealand are from Spring, 1984. For New South Wales, Summer 1984–1985 (Cape Banks) unless otherwise noted. Values are $\bar{x} \pm 1$ S.E. Sample sizes in parentheses

New Zealand		
Adult 2° laminae (all)		9.28+0.44 (19)
Deep (>10 m)		9.41+0.60 (13)
Shallow (<10 m)		8.99+0.54 (6)
Juveniles		10.16+0.52 (2)
Stipes		2.59+0.21 (6)
Sori (1986)		10.79+1.26 (5)
Non-soric tissue adjacent to sori (1986)		11.93+2.05 (5)
Non-soric 2° laminae adjacent to soric laminae (1986)		10.62+0.89 (5)
New South Wales		
Adult 2° laminae		
All sites (summer)		5.48+0.56 (19)
Cape Banks		
summer		6.77+0.90 (9)
winter		5.63+0.90 (5)
Stipes		1.48+0.31 (4)
1° laminae		1.43+0.32 (4)
Juveniles		
summer		8.87+1.07 (10)
winter		8.93+0.55 (5)
South Australia (Winter 1985)		
Adult laminae (all)		7.46+0.86 (14)

0.5). The reproductive receptacles of *Carpophyllum maschalocarpum* in New Zealand may be lower in phenolic content than the vegetative tissues (Table 1). However, the difficulty in accumulating enough receptacles to do the analyses resulted in very small sample sizes.

The majority of species examined in this study did not show either significant spatial or temporal variation in phenolic levels (Table 1 and 2). Moreover (and importantly), those that did still generally contained very high levels of phenolics relative to plants from the northeast Pacific. Samples from only six species contained levels comparable to phenolic-poor species from the northeast Pacific. These were *Phyllospora comosa* from Warrah in New South Wales, *Sargassum linearifolium* in the winter in New South Wales, stipes and primary laminae of *Ecklonia radiata*, *Macrocystis angustifolia* and *Durvillaea potatorum* from Victoria, and *Lessonia variegata* in New Zealand.

Changes in phenolic levels in "drift" algae

There is no change in the phenolic content of thalli of either *Ecklonia radiata* or *Sargassum vestitum* when detached and placed in cages or plastic bins (or tethered) for a period of up to 2 weeks (Fig. 3a, b; Single-factor ANOVA for both species in Fig. 3b; both $P \geq 0.05$). Herbivores which feed on drift plants of these two species will face plants which contain similar phenolic levels as attached algae. Phenolic levels in *Ecklonia radiata* in experiment 2 were high relative to previous samples at Cape Banks, but were repre-

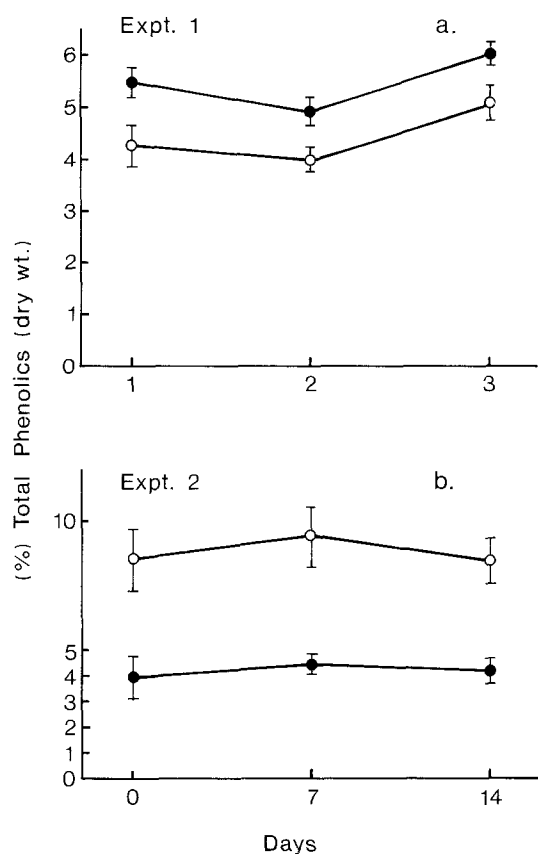


Fig. 3a, b. Changes in phenolic content of "drift" algae. *Ecklonia radiata* – ○; *Sargassum vestitum* – ●. No change in phenolic content over time in either species in Experiment 2 is significant, as determined by single factor ANOVA. Data in Experiment 1 are non-independent over time, and were not analyzed statistically. Experiment 1; sample size (n)=3 for each day for *Ecklonia radiata*, $n=4$ for *Sargassum vestitum*. Experiment 2; $n=5$ for all days except day 14 for *E. radiata* (2 plants lost, $n=3$). Data are $\bar{x} \pm 1$ S.E.

sentative of levels in this species during the summer of 1987–1988 (Steinberg, unpublished work).

Discussion

Secondary metabolites and chemical defenses in Australasian and North American brown algae

Brown algae in the orders Fucales and Laminariales in temperate Australasia typically contain very high levels of polyphloroglucinols (Table 1; Fig. 2) – levels consistently much higher than are found in species from these orders in North America (Geiselman 1980; Steinberg 1985). The majority of species analyzed in this paper contain at least the amount of phenolics found in "phenolic-rich" species from California and the northeast Pacific (Steinberg 1985), and many species contain 2–3 times these levels. These differences are exacerbated when one restricts the comparison to sublittoral species, since many of the phenolic-rich fucoids in North America (*Fucus*, *Pelvetia*, *Ascophyllum*, etc.) are primarily intertidal species.

Furthermore, although polyphenolics appear to be the only likely major chemical deterrent against herbivores in

Table 4. Presence of non-polyphloroglucinol, non-polar secondary metabolites in fucoid brown algae from temperate Australia and New Zealand

Species	Reference
Fam. Cystoseiraceae	
<i>Cystophora moniliformis</i>	Kazlauskas et al. 1978; Ravi et al. 1982; van Altena 1987
<i>C. torulosa</i>	Gregson et al. 1977
<i>C. scalaris</i>	Kazlauskas et al. 1981
<i>C. congesta</i>	Kazlauskas et al. 1981
<i>C. expansa</i>	Kazlauskas et al. 1981
<i>C. monilifera</i>	Kazlauskas et al. 1981
<i>Acrocarpia paniculata</i>	Kazlauskas et al. 1982
<i>Landsburgia quercifolia</i>	W. Fenical and P. Steinberg unpublished work
<i>Caulocystis cephalornithos</i>	Kazlauskas et al. 1980
Fam. Sargassaceae	
<i>Sargassum bracteolosum</i>	I. van Altena and P. Steinberg, unpublished work
<i>S. sinclairii</i>	W. Fenical and P. Steinberg, unpublished work

kelps and fucoids from North America (Faulkner 1984, 1986), many fucoids in temperate Australasia are rich in non-polar, non-polyphenolic secondary metabolites (Table 4). These compounds, such as terpenoids and prenylated or alkylated phenolics, can comprise >1% of the dry weight of the thallus of a number of the species analyzed in this paper (Ravi et al. 1982; Kazlauskas et al. 1980). These compounds are similar to metabolites from tropical algae which are deterrent against herbivores (Hay et al. 1987a, b).

Thus the secondary metabolites found in the dominant component of algal communities (Womersley 1981a, b; Choat and Schiel 1982; Dayton 1985; Kirkman 1984; Schiel and Foster 1986) in the northeast Pacific and (more generally) North America differ dramatically, both quantitatively and qualitatively, from those of similar algae in temperate Australasia. These metabolites – polyphloroglucinols, terpenoids, and alkylated or prenylated phenolics – are the major chemical defenses known from marine brown algae in both temperate (Geiselman and McConnell 1981; Steinberg 1985, 1988) and tropical (Hay et al. 1987a, b) systems. The food quality of a major part of the algal flora faced by marine herbivores in Australia and New Zealand is therefore very different from that faced by herbivores in North America. These differences should have major consequences on the feeding biology of Australasian herbivores.

These conclusions are not significantly modified by intraspecific variation in phenolics in these algae, or by herbivores feeding on drift algae. Although several of the algae studied here exhibited significant spatial, temporal, or intraplant variation, the upper and lower limits of the variability were still generally at high levels. For example, although spatial variation in *Cystophora moniliformis* was highly significant (Table 1 and 2), all plants in this species still had higher levels of phenolics than almost any species in California. Intraspecific variability in phenolic levels only

resulted in very low phenolic levels for some plants in three species; *Phyllospora comosa*, *Sargassum linearifolium*, and *Ecklonia radiata*. In addition, since phenolic levels in "drift" *E. radiata* and *S. vestitum* are maintained for at least two weeks, herbivores feeding on drift algae should still usually face chemically-rich plants.

Geographical and taxonomic patterns in algal phenolic production, and plant/herbivore evolution

Biogeographical variation in plant/herbivore or predator/prey interactions has played an important role in the development of marine ecology and evolutionary biology (Bakus 1969; Vermeij 1978; Gaines and Lubchenco 1982). The general conclusions of these studies are that the intensity of predation or herbivory, and the frequency or diversity of defensive traits of the prey, are greater in the tropics than in temperate regions (Vermeij 1978; Fenical 1980; Gaines and Lubchenco 1982; Steneck 1986). Comparisons among temperate areas are less common, but generally differences are considered to be less than those between temperate and tropical regions (Vermeij 1978; Gaines and Lubchenco 1982).

Sufficient data on the phenolic content of brown algae in the Orders Fucales and Laminariales are now available to allow comparisons to previous observations. These data (also see Ragan and Glombitza 1986, Tables 15, 17) indicate that biogeographical variation in polyphenolic compounds differs considerably from previous patterns.

Firstly, differences among temperate regions can be similar in magnitude to previously described tropical/temperate gradients. Temperate North America differs significantly from temperate Australasia (this paper). This appears true of both the west (Steinberg 1984; 1985; van Alstyne 1988) and east (Geiselman 1980) coasts of North America. Other temperate regions are less well known, or have been investigated by a number of workers using a variety of techniques, thus making comparisons more difficult (Ragan and Glombitza 1986). However, temperate Europe (Ragan and Glombitza 1986), South Africa (Anderson and Velimirov 1982), and perhaps the northwest Pacific (Estes and Steinberg 1988) would appear to be similar to North America in having a mixture of phenolic-rich and phenolic-poor species. Phenolic levels in South American algae are not known but the dominance of genera such as *Macrocystis*, *Lessonia*, and *Durvillaea*, and the paucity of furoids (Nizammuddin 1970), suggests a phenolic-poor flora.

Much of the variation in phenolic content among temperate species also follows taxonomic lines. Furoids are generally rich in phenolic content, kelps (Laminariales) are typically poor (Results; Steinberg 1985; Geiselman 1980). The most notable exception to this general pattern is the kelp genus *Ecklonia*, which appears to be consistently high in phenolics (Tables 1-3; Katayama 1956; Anderson and Velimirov 1982). This is an ecologically important exception, given the abundance of *Ecklonia* in the Southern Hemisphere. Other exceptions include the phenolic-rich kelps *Dictyonium californicum* and *Agarum* spp. (Steinberg 1985, Estes and Steinberg 1988), and examples of seasonal, spatial, or intraplant variation in various kelps or furoids (Geiselman 1980; Steinberg 1984; Johnson and Mann 1986; Ragan and Glombitza 1986; this paper). This taxonomic variation also correlates with depth-related patterns in the Northern-Hemisphere, since furoids there are generally

most abundant in the littoral zone, whereas kelps are most abundant in the lower littoral and sublittoral. Phenolic levels in Australasian algae do not appear to vary strongly with depth (e.g., Table 3). Production of non-polar secondary metabolites by furoids in Australasia (and elsewhere in the world [Faulkner 1984, 1986]) also shows a taxonomic pattern, with species in the families Cystoseiraceae and Sargassaceae rich in terpenoids and/or prenylated phenolics (Table 4).

The second major difference to previously described biogeographical patterns in defensive traits in marine organisms is that temperate brown algae generally contain higher levels of polyphenolics than do related tropical plants (Steinberg 1986). This has now been confirmed for a variety of tropical locations (Steinberg 1986; Paul and Steinberg in prep.). This result indicates that the high levels of phenolics typically found in temperate furoids are not a fixed trait, characteristic of all furoids (also shown by seasonal variation in *Fucus vesiculosus* [Geiselman 1980] and *Sargassum linearifolium* [Table 1]). Non-polar secondary metabolites occur in both tropical and temperate brown algae (Table 4; Gerwick and Fenical 1981; Faulkner 1984).

Many processes may underly these general patterns in the production of secondary compounds by brown algae. Estes and Steinberg (1988) have argued that subtidal algal systems (particularly kelps) in the northeast Pacific evolved under a relatively mild regime of herbivory, due to the influence of sea otters as predators of invertebrate herbivores. They suggested, however, that herbivory may have been more intense in Australasia over the recent evolutionary past, and this may have selected for high levels of chemical defenses in the algae there. The apparently higher diversity of herbivorous fishes in temperate Australasia (Choat 1982) is interesting in this regard. Estes and Steinberg's (1988) ideas do not explain the low levels of polyphenolics in tropical furoids.

Alternative scenarios to this include ascribing the variation to historical or biogeographical "accidents". However, it is difficult to understand why such dramatic differences in levels of polyphenolics would be maintained in the absence of some sort of selection pressure(s), especially when considerable intraspecific and intrageneric variation exists (Results; Steinberg 1986).

Most theories which seek to explain the evolution of herbivores and the chemical defenses of plants use as a basis local ecological conditions which are assumed to have persisted over the recent evolutionary past (Feeny 1976; Rhoades 1979; Fox 1981; Coley et al. 1985). I show here that while local variation in secondary metabolites in brown algae exists, the major source of variation is due to differences in geography and/or taxonomy (primarily at the ordinal level). Thus rather than considering brown algae and their herbivores as a system of numerous local pairs or small groups of interacting species (as in the original concept of coevolution), I suggest that the system is a very diffuse one, in which many species of plants interact with many species of herbivores over broad spatial and temporal scales (Fox 1981; Futuyama and Slatkin 1981). If this model is correct, then any general explanation for the evolution of brown algae and their herbivores must take into account large scale biogeographical and taxonomic differences.

A recent symposium (Dodson and Westoby 1985) examined the differences between Australian and North American ecosystems. In general the conclusions of the contri-

buters were equivocal (Morrow 1987). I show here that there are important differences in the levels of putative chemical defenses found in brown algae between North America and Australia. In a separate paper, we discuss differences in the responses of the herbivores to these compounds (Steinberg and van Altena unpublished work).

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