Evolutionary consequences of food chain length in kelp forest communities

(biogeography/coevolution/herbivory/phlorotannins/predation)

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ABSTRACT Kelp forests are strongly influenced by macroinvertebrate grazing on fleshy macroalgae. In the North Pacific Ocean, sea otter predation on macroinvertebrates substantially reduces the intensity of herbivory on macroalgae. Temperate Australasia, in contrast, has no known predator of comparable influence. These ecological and biogeographic patterns led us to predict that (i) the intensity of herbivory should be greater in temperate Australasia than in the North Pacific Ocean; thus (ii) Australasian seaweeds have been under stronger selection to evolve chemical defenses and (iii) Australasian herbivores have been more strongly selected to tolerate these compounds. We tested these predictions first by measuring rates of algal tissue loss to herbivory at several locations in Australasian and North Pacific kelp forests. There were significant differences in grazing rates among sea otter-dominated locations in the North Pacific (0–2% day^{-1}), Australasia (5–7% day^{-1}), and a North Pacific location lacking sea otters (80% day^{-1}). The expectations that chronically high rates of herbivory in Australasia have selected for high concentrations of defensive secondary metabolites (phlorotannins) in brown algae and increased tolerance of these defenses in the herbivores also were supported. Phlorotannin concentrations in kelps and fucoids from Australasia were, on average, 5–6 times higher than those in a comparable suite of North Pacific algae, confirming earlier findings. Furthermore, feeding rates of Australasian herbivores were largely unaffected by phlorotannins, regardless of the compounds' regional source. North Pacific herbivores, in contrast, were consistently deterred by phlorotannins from both Australasia and the North Pacific. These findings suggest that top-level consumers, acting through food chains of various lengths, can strongly influence the ecology and evolution of plant–herbivore interactions.

The extent to which biological communities are organized by top-down vs. bottom-up forces has been a topical question in ecology for more than 3 decades (1–3). The top-down view is that consumers control the abundance and diversity of species at lower trophic levels, whereas the bottom-up view is that consumers are limited by the upward acting effects of resources (e.g., energy and nutrients). In systems with strong top-down linkages (4), high-level predators can have influences extending to the base of the food web. Complex interactions of this sort, best known in aquatic systems (5–8), have been popularized as trophic cascades (4, 9).

Effects of predator-driven trophic cascades on autotrophs should vary depending on whether the number of trophic levels is odd or even (10, 11). The logic underlying this expectation presupposes that (i) the system is under top-down control, and (ii) exploitative competition and predation (or herbivory) are

consistently important structuring processes throughout the food web. Under these conditions, we would predict that top-level consumers are resource limited. Consequently, the next lower trophic level should be consumer limited, in turn causing the level below that (if one exists) to again be resource limited. Looking downward through the food web from this very generalized perspective, a pattern emerges of strongly interacting couplets of adjacent trophic levels. Given these circumstances, the interactive coupling between plants and herbivores should be strong in even-numbered systems and weak in odd-numbered systems, a prediction recently substantiated for riverine communities (7).

Ecological forces generated by trophic cascades may well affect selection on the participating species when they persist over evolutionary time scales. Such evolutionary effects are most likely to occur within strongly interacting couplets of adjacent trophic levels. This model predicts that in even-numbered food webs plants and their herbivores should have strong selective influences on each other. More specifically, the plants should evolve defenses against herbivory and the herbivores, in turn, should evolve ways of coping with or overcoming these defenses. Thus, in even-numbered food webs there is the potential for coevolution (diffuse or pairwise; see refs. 12 and 13) between plants and their herbivores. Conversely, reciprocal selective influences between plants and their herbivores should be weak or absent in odd-numbered food webs. Here we summarize observations and experiments from kelp forest communities, done on a biogeographical scale, which support these predictions. This synthesis draws from earlier ideas (14) and findings (15, 16) as well as more recent studies designed to test the predictions listed above.

The System

Like most biological communities, kelp forests contain a rich diversity of species, forms, and ecological interactions. In addition, the structure and function of most communities vary over a range of spatial and temporal scales. However, relatively few "keystone species" (17) and a limited number of exceptionally strong interactions may structure much of this diversity. With this perspective in mind, we have proposed that kelp forests of the temperate North Pacific and Australasia have fundamentally different trophic structures (14). The North Pacific is a three-tiered (odd-numbered) system, dominated by the top-down force of sea otter (Enhydra lutris) predation on herbivorous sea urchins. Extensive evidence now exists for the general importance of this interaction in the maintenance of kelps and other macroalgae (18). Australasian kelp forests, in contrast, appear to be 2-tiered systems. While top-down influences of predators on herbivores have been sought or suggested (19), none of comparable importance to that of the sea otter have been found (20–22). This structural disparity

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between North Pacific and Australasian kelp forests probably has existed since the late Miocene/early Pliocene (14, 23, 24), during which time regional biotas have been isolated from one another by the tropical Pacific (25).

These ecological and biogeographical patterns, the hypothesized influence of generalized food web structure on the intensity of plant–herbivore interactions, and extensive evidence for the importance of secondary metabolites as antiherbivore defenses in marine algae (26, 27) led us to predict the following: Relative to the North Pacific Ocean the intensity of herbivory should be greater in temperate Australasia, thus resulting in stronger selection on Australasian seaweeds to produce chemical defenses, and in turn stronger selection for tolerance to these compounds in Australasian herbivores. Below we summarize supporting evidence for these predictions.

Intensity of Herbivory

Our model is predicated on the idea that the intensity of herbivory varies in different ecological settings. Two spatial contrasts are useful in evaluating this idea. The first is between areas of the North Pacific Ocean with and without sea otters. If kelp forest communities in the North Pacific are three-tiered systems under top-down control with sea otters as the principal controlling agents at the top of the food web, then removal of sea otters should increase the rate of plant tissue loss to herbivory. The second relevant contrast is between Australasian kelp forests and those of the North Pacific in which sea otters are present. If the intensity of herbivory has been lower in the North Pacific over recent evolutionary time, this difference should be evident when the systems are in their presumed historically natural states.

These predictions were tested by *in situ* measurements of macroalgal tissue loss to herbivory. We did this by attaching 20- to 40-g pieces of locally common brown seaweeds (kelps and fucoids) to brass bars, placing the bars at random locations on the sea floor at depths of 5–10 m, and measuring the change in algal mass after 24 hr. Each experiment included five uncaged replicates and three caged (herbivore exclusion) replicates for each of four to six brown algal species. The algae used in these experiments varied among regions (because of availability) but included species that spanned the range of phlorotannin concentrations for each particular region. For this reason, average and maximum phlorotannin concentrations were higher in the Australasian experiments. The experiments were repeated at five randomly selected sites at three locations each in New Zealand (Goat Island Reserve, Great Barrier Island, Dunedin) and Alaska's Aleutian Islands (Amchitka, Adak, and Shemya islands). Sea otters were abundant

(near equilibrium density) at Amchitka and Adak islands, whereas they were absent from Shemya Island (where they had been hunted to extinction during the 18th and 19th centuries in the North Pacific fur trade). Each location spanned 10–20 km of exposed outer coast habitat.

Interlocational variation in the intensity of herbivory was analyzed by single factor ANOVA on the rates of tissue loss from uncaged algae. Because (*i*) mass changes of the caged algae were small relative to those of the uncaged treatments, and (*ii*) the rates of tissue loss in the caged algae did not vary significantly among species or locations (2-way ANOVA), data from the caged controls were not included in the following analyses.

Rates of algal tissue loss to herbivory were strikingly different among locations and the directions of these differences were consistent with our expectations (Fig. 1). The average loss rate at Shemya Island (sea otters absent) was 30–100 times greater than it was at the otter-dominated islands of Adak and Amchitka. This finding (*i*) supports the hypothesis that sea otters limit the intensity of herbivory on macroalgae and (*ii*) is consistent with larger scale patterns of plant and herbivore abundance between these locations (18). Second, loss rates in New Zealand were 3–10 times greater than those at Alaskan locations with sea otters, supporting the hypothesis that grazing intensity is higher in Australasian than in North Pacific kelp forests when these systems are in their presumed historically natural states.

Another informative contrast in grazing rates is between two-tiered systems in Australasia and the North Pacific. If Australasian algae have evolved higher levels of chemical defenses against their herbivores, then the rate of tissue loss to herbivory should be significantly greater in the North Pacific when both systems are faced with unregulated herbivory. Grazing rates in North Pacific kelp forests without sea otters (Shemya Island) were significantly greater than they were in New Zealand (Fig. 1), thus supporting this prediction. Recent experiments in southeast Australia and California suggest patterns similar to those described here for Alaska and New Zealand (J.A.E. and P.D.S., unpublished data).

Plant Defenses

Consistent with our second prediction, and confirming earlier studies (15), average levels of phlorotannins—the principal secondary metabolites in temperate brown algae (27–29)—are ≈5 times greater in kelps (order Laminariales) and rockweeds (order Fucales) from Australasia than from the North Pacific Ocean (Fig. 2). Nonpolar metabolites, such as terpenoids, also appear to be common in Australasian brown algae (15).
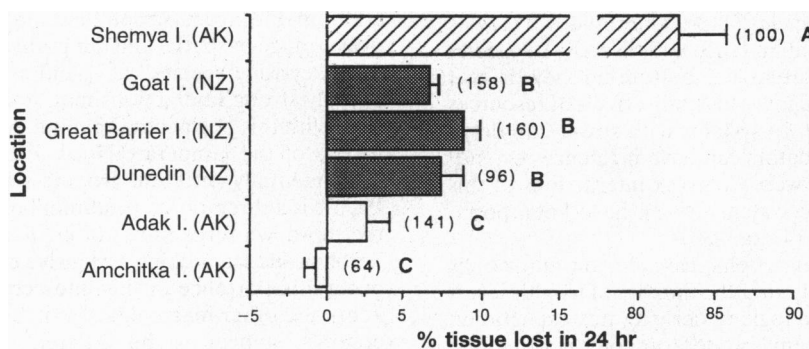

FIG. 1.   Results of *in situ* grazing assays (mean + 1 SE of percentage algal tissue lost 24 hr^{-1}) from New Zealand and Alaska. Sample size (*n*) for each location is shown in parentheses. Sea otters were at or near equilibrium densities at Adak and Amchitka islands (open bars) and were absent at Shemya Island (cross-hatched bar) and all New Zealand locations (solid bars). Grazing rates at locations sharing a common letter (A, B, or C) did not differ significantly at $P < 0.05$, as determined by 1-way ANOVA followed by Duncan's multiple range test [ANOVA for arcsin(% tissue lost to grazing)$^{1/2}$ among locations; $F_{5,734} = 310.3$; $P \ll 0.0001$].

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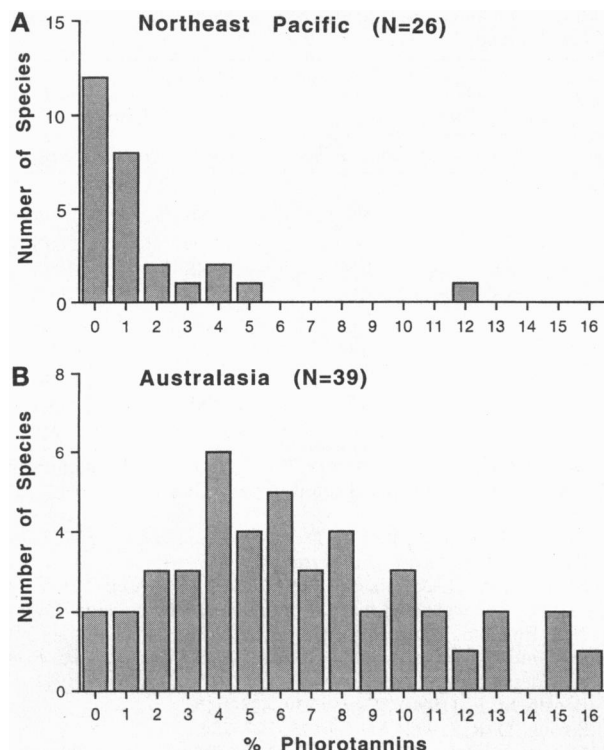
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FIG. 2. Frequency distribution of mean levels of phlorotannins for sublittoral fucoids and kelps from the temperate North Pacific Ocean (*A*) and Australasia (*B*). Data are percentage dry weight phlorotannins, averaged across different seasons, sites, etc., where relevant (refs. 15 and 16; P.D.S. and J.A.E., unpublished data). N, number of species analyzed for each region.

Herbivore Tolerance to Plant Defenses

The influence of phlorotannins on feeding by kelp forest herbivores was evaluated with compounds extracted (16, 28) from the North Pacific brown seaweeds *Agarum cribrosum* and *Dictyoneurum californicum* and the New Zealand brown seaweeds *Ecklonia radiata* and *Carpophyllum maschalocarpum*. Feeding deterrence by the phlorotannins was tested against three common invertebrate herbivores from California (the gastropods *Tegula funebralis* and *Tegula brunnea* and the echinoid *Strongylocentrotus purpuratus*) and four from New Zealand (the gastropods *Turbo smaragdus* and *Cookia sulcata* and the echinoids *Centrostephanus rodgersii* and *Evechinus chloroticus*). One echinoid or 5–15 gastropods (depending on species) were used per experimental unit (20- to 40-liter plastic aquaria with flowing seawater). The tests were done as paired choice experiments in which consumption rates of agar disks lacking phlorotannins were compared with consumption rates of otherwise similar disks in the same aquaria containing phlorotannins. Concentrations of phlorotannins in the disks were either 5% or 13.4% by disk dry weight, selected to parallel those found naturally in seaweeds (15, 28). These experiments allowed us to (*i*) isolate the effects of phlorotannins from other plant characters and (*ii*) evaluate the potentially confounding influences of biogeographic region and algal species on the effects of phlorotannins.

The effects of phlorotannins from *D. californicum* on herbivores from New Zealand and California illustrate the typical pattern (Fig. 3). Feeding by California herbivores was deterred at both phlorotannin concentrations. In contrast, feeding by New Zealand herbivores was mostly undeterred, and for one species (*T. smaragdus*) it was significantly enhanced. This pattern was generally similar for the other phlorotannins tested (Table 1). Taken across all experiments, the proportion
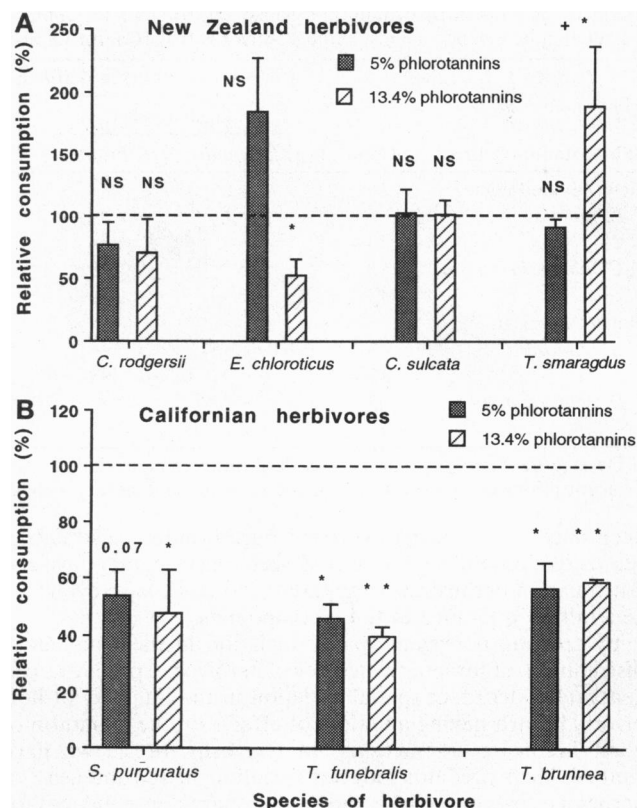

FIG. 3. Bioassays for effects of phlorotannins from the California kelp *D. californicum* as feeding deterrents against New Zealand (*A*) and Californian (*B*) invertebrate herbivores. Phlorotannins were tested against four herbivores from New Zealand and three from California (see text). Significant feeding deterrence (as determined by one-tailed *t* tests) is indicated by * ($P < 0.05$) or ** ($P < 0.01$). Significant feeding enhancement at $P < 0.05$ is indicated by +*. NS, no significant difference in consumption rates between disks with and without phlorotannins. Exact probability is shown when $0.10 > P > 0.05$. Data are means + 1 SE, calculated relative to the amount consumed of disks lacking phlorotannins (dashed line). Sample sizes per experiment, 9–13.

of tests in which phlorotannins had demonstrably deterrent effects differed significantly between herbivores from California and New Zealand [tested by a normal approximation to binomial comparing the proportion of significant results (paired *t* tests) between California and New Zealand herbivores; $\alpha = 0.05$ or 0.01 in the *t* tests; $P < 10^{-5}$ for both cases]. Conversely, using the same tests and test criteria, we were unable to demonstrate significant differences between phlorotannins from the two regions ($P > 0.05$). Thus, while the response to phlorotannins by herbivores differed significantly between Australasia and the North Pacific, there was no consistent qualitative difference in the effects of phlorotannins from the two regions.

Discussion

These experiments and observations, done reciprocally and on a biogeographic scale, support earlier predictions (14) that kelp forest communities in Australasia and the North Pacific Ocean differ in both their ecological structure and its evolutionary consequences. Kelp forests in the North Pacific and New Zealand, although both strongly influenced by top-down forces, have different trophic structures. The former is an odd-numbered (three-tiered) system, whereas the latter is even numbered (two-tiered). Consequently, the intensity of herbivory is significantly greater in Australasia and probably has

Table 1. Results of phlorotannin bioassay experiments for compounds extracted from northeast Pacific and New Zealand brown algae tested for feeding deterrence against three herbivores from California and four from New Zealand

Phlorotannin source	Conc.	California herbivores			New Zealand herbivores			
		Gastropods		Echinoid	Gastropods		Echinoids	
		T. funebralis	*T. brunnea*	*S. purpuratus*	*C. sulcata*	*T. smaragdus*	*E. chloroticus*	*C. rodgersii*
New Zealand algae								
E. radiata	5	*	*	*	***	NS	NS	NS
	13.4	**	**	*	***	*	*	NS
C. maschalocarpum	5	*	NS	NS	NS	NS	NS	NS
	13.4	NS	**	*	NS	*	NS	NS
North American algae								
A. cribrosum	5	0.073 (15)	**	*	NS	—	NS	NS
	13.4	*	NS	NS (6)	NS	—	NS	NS
D. californicum	5	*	*	0.057	NS	NS	NS	NS
	13.4	**	**	*	NS	+	*	NS

Deterrence by phlorotannins was determined by one-tailed paired t tests. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. NS, not significant. Concentrations of phlorotannins (Conc.) are percentage dry weight of agar disks. $n = 8$–14 except as indicated in parentheses.

been since at least the late Tertiary. Furthermore, Australasian seaweeds contain high levels of secondary metabolites and Australasian herbivores, in apparent response, have evolved a generalized tolerance to these compounds.

By creating persistent spatial variation in the abundance, distribution, or foraging efficiency of herbivores, predators can generate concordant spatial variation in the intensity of herbivory, in turn having a variety of effects on the evolution of plant–herbivore interactions. In the kelp forests we have studied, such predator-induced variation in the intensity of herbivory appears to have had evolutionary consequences for plant–herbivore interactions at both the regional scale—between Australasia and the North Pacific—as well as the local scale of different depths in the Aleutian Islands (14). In both instances, phlorotannin concentrations are substantially higher for algal species that live among the greater abundances of herbivores. On tropical coral reefs, the correlation between spatial variation in the intensity of herbivory and the distribution of herbivore-resistant algae (30–33) may also in part be a consequence of predators limiting the distribution or foraging behavior of herbivores (32, 34). At smaller spatial scales, Hay and others (26, 27) have argued that escape from predation ultimately is responsible for the evolution of tolerance to seaweed chemical defenses by "mesograzers," small herbivores that avoid being eaten by living on chemically rich seaweeds that deter larger consumers. Predator avoidance also has been proposed as a major factor in the evolution of feeding specialization in herbivorous insects (ref. 35, although see also ref. 36). These examples suggest that variation in the intensity of predation, and consequent variation in trophic structure, is likely to have strong effects on the evolution of plant–herbivore interactions in a number of systems, with implications ranging from plant morphology and chemistry to grazer physiology and behavior.

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