Predation, Herbivory, and Kelp Evolution

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Abstract.—We propose that the kelps (Laminariales) radiated in the North Pacific following the onset of late Cenozoic polar cooling. The evidence is that (1) extant kelps occur exclusively in cold-water habitats; (2) all but one of 27 kelp genera occur in the North Pacific, 19 of these exclusively; and (3) limpets and herbivorous marine mammals obligately associated with kelps or other stipitate brown algae appeared late in the Cenozoic, even though more generalized forms of both groups are much older. We propose, further, that sea otters and perhaps other groups of benthic-feeding predatory mammals, whose late Cenozoic distributions all were limited to the North Pacific, created an environment for the evolution of kelps in which the intensity of herbivory was unusually low. We hypothesize that this interaction created predictable differences among habitats in the intensity of herbivory on several spatial scales, with resulting trade-offs between anti-herbivore defenses and plant competitive abilities in their respective floras. Sea otters incur time and energy costs for diving, resulting in depth-related reductions to foraging efficiency and thus increased sizes and densities of herbivorous sea urchins. Thus, the deep-water flora is well defended, but competitively subordinate, compared with the shallow-water flora. Similarly, we argue that during the same period of earth history, predation had less of a limiting influence on herbivorous invertebrates in the temperate southwestern Pacific. We hypothesize that (1) consequent biogeographical differences in the intensity of herbivory may have selected the phenolic-rich brown algal flora in temperate Australia/New Zealand; and (2) tightly coevolved plant/herbivore interactions may explain why Australian and New Zealand herbivores are undeterred by phenolics and why other classes of secondary compounds in the Australian/New Zealand flora significantly deter herbivores.

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Introduction

Highly conspicuous assemblages of large brown algae, often termed "kelp beds" or "kelp forests," are a typical feature of the rocky coasts of cool seas. The kelp-like plants are of two main groups, the true kelps (Order Laminariales) and the rockweeds (Order Fucales). Large-scale distributional patterns are now well known for these taxa, as are many physical and biological influences that determine small-scale distributional patterns for the more common forms (Foster and Schiel 1985; Dayton 1985b; Schiel and Foster 1986).

The theme of this essay is kelp evolution. Our approach will be similar to that employed by Vermeij (1977) in his treatment of predation and molluscan shell evolution and by Steneck (1983) in his study of herbivory and adaptive trends in calcareous algal crusts. That is, we formulate a modern-day view of kelp forest communities from distributional patterns and known ecological processes and then reconstruct past events from the record of earth history, while assuming that important ecological processes operated in the past as they do now.

We go about this exercise in four steps. First we define the system. Of the many species presently residing in coastal waters at temperate latitudes, we focus on the kelps, their important herbivores, and the predators of those herbivores. Second, we discuss when and where these groups arose and how they radiated. Third, we summarize ecological interactions of known or suspected significance to kelp forest communities, from which we propose a model for the modern-day workings of the system. Finally, we combine this information with a global comparison of kelp forests, from which we speculate on the evolution of marine plant/herbivore interactions at temperate latitudes.

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We suggest (1) that the kelps had a North Pacific center of origin; (2) that they radiated extensively within the North Pacific during the late Cenozoic; and (3) that they evolved in an environment in which the intensity of herbivory was low. We further hypothesize that elsewhere in the world during this same period of earth history, the intensity of herbivory was greater, thus resulting in stronger interactions through evolutionary time between plants and their herbivores in those regions. Recognizing the speculative nature of these ideas, whenever possible we suggest testable predictions and discuss alternative explanations for the observed patterns.

Constructing a model based on both ecology and history poses a procedural dilemma, since the rules of inquiry and inference are vastly different between these disciplines (Gould 1986). Ecology has become an experimental science, seeking to understand recurrent processes through the control of variation and the replication of predictable results. History, on the other hand, comprises singular past events, is unrepeatable and uncontrolled, and has no real predictive power. Our efforts require the amalgamation of both disciplines, for neither by itself can untangle the larger issues addressed herein.

The Food Web

We begin by drawing some geographic and taxonomic limits to the scope of our paper. We focus initially on the North Pacific Ocean. Our view of the system shall be restricted to a simple food web, with sea otters (*Enhydra lutris*) at the top (the carnivores), sea urchins (*Strongylocentrotus* spp.) in the middle (the herbivores), and kelp at the bottom. We assume this view because it contains the most conspicuous forms at each trophic level, or did until recently; and where they co-occur, there are strong linkages (Paine 1980) between sea otters and sea urchins (Lowry and Pearse 1973; Estes et al. 1978; Duggins 1980; Breen et al. 1982) as well as between sea urchins and kelp (Lawrence 1975; Dayton 1985b; Foster and Schiel 1985; Harrold and Pearse in press). The elements of this food web—sea otters, sea urchins, and kelp—appear to be disproportionately important to community organization, or as Dayton (1972: p. 85) put it, they are the system's "foundation species."

Biogeography and Evolutionary History

Kelp

There is virtually no fossil record for the kelps (Clayton 1984). We know only of one record, *Julescrania* (Parker and Dawson 1965), from the Miocene. However, the time and place of kelp origin and diversification can be inferred from paleoclimatological patterns, along with marine climatic conditions typical of where the kelps presently occur; the evolutionary histories of kelp associates for which there is a fossil record; and extant geographic distributions of kelp species.

Paleoclimatology.—Until as recently as the Middle Miocene, marine faunas with tropical/subtropical aspects occurred in the North Pacific (Addicott 1970). For example, *Dosinia* (Pelecypoda) and *Ficus* (Gastropoda) are found in Middle Miocene deposits near Kodiak Island (about 57 degrees North latitude), which at the time were no more than several hundred km south of the Bering Land Bridge, the northernmost extent of the Pacific water mass (Hopkins 1967). Today the respective northernmost extents of *Dosinia* and *Ficus* are 27 degrees and 22 degrees North (Addicott 1969). With the single exception of *Eisenia arborea*, which ranges south to about 25 degrees North, there are no kelps in the eastern North Pacific whose ranges (Druehl 1969) presently overlap those of *Dosinia* and *Ficus*.

These patterns suggest that climatic conditions in the North Pacific Ocean were generally unsuitable for kelps until the Middle to Late Miocene, at which time there began a strong polar cooling trend (Durham 1950; Clark 1971; Luyendyk et al. 1972; Savin et al. 1975; Frakes 1979; Wolfe and Poore 1982). For example, at the Oligocene/Miocene boundary, the 13 degrees C isotherm in midwinter occurred at about 65 degrees North. Presently this isotherm occurs at about 34 degrees North.

The history of kelp associates.—Marine plants and herbivorous limpets (Patellogastropoda) are common components of Recent rocky nearshore communities. Patellogastropoda is an ubiquitous and diverse clade with numerous taxa forming specific associations with particular substrata. In many regions, limpets form close associations with two groups of marine plants, kelps and seagrasses. In each case the limpets are distinguished by unique morphologies that often can be recognized in the fossil record. The kelp associates have a distinct "saddle-shaped" shell aperture which conforms the limpet to the stipe of its algal host when their longitudinal axes are parallel (Carlton 1976; Lindberg 1976). There are five known limpet species with saddle-shaped shells (Powell 1973; Christians 1975a,b): two from the North Pacific (*Lottia instabilis* and *Rhodapatela rosea*), one from the North Atlantic (*Helcion pellucidus*), one from South Africa (*Patella compressa*), and one from South America (*Scurria scurria*). These represent four subfamilies, two in the Lottiidae and two in the Patellidae.

Seagrass limpets also have a distinctive shell morphology, typified by parallel lateral margins and elevated anterior and posterior portions of the aperture (Lindberg 1982). Like the kelp limpets, seagrass limpets have evolved independently in several families (D. R. Lindberg, unpubl. ms.).

Patellogastropod limpets are known from the Mesozoic. Most have oval apertures suggesting non-plant substrates, although species with plant-associated morphologies are present. Saddle-shaped kelp limpets date from the Pleistocene/Recent in all instances (D. R. Lindberg, pers. comm.). However, seagrass limpets date from at least the Eocene. Cossmann and Pissarro (1910–1913) identified over 15 species of limpets from the Eocene of the Paris Basin which are now recognized as having lived on marine angiosperms (Lindberg, unpubl. ms.). Other radiations of seagrass limpets occurred in the Miocene/Pliocene of both the Caribbean and North Pacific (Lindberg, unpubl. ms.). Moreover, unlike the kelps, seagrasses left fossil records. Earliest known seagrasses date from the mid- to Late Cretaceous, and marine angiosperms apparently have been common in many areas of the world at least since the Eocene (den Hartog 1970; Brasier 1975; Eva 1980; Lumbert et al. 1984). Thus the seagrasses are an old flora and the age of their associated limpet fauna reflects this. Although similar temporal correlations cannot be made between kelp-associated limpets and fossil kelps, kelp-associated limpets would be expected to occur much earlier in the fossil record if the kelp flora were an old one.

If kelp-associated limpets existed before the Pleistocene, the northeastern Pacific would be a good place to look for them. Both kelps and limpets are abundant in this region. Furthermore, a diverse limpet fauna is known to have inhabited the region for more than 65 m.y. (Lindberg 1983, in press; Lindberg and Hickman 1986). However, most known limpet species have typical oval apertures; the kelp associates appear only in the last 3 m.y. This appears to be a world-wide pattern. We thus conclude that the sudden appearance in the Pleistocene of limpets with shell forms reflecting associations with the large brown algae indicates that a proliferation of kelps did not occur until comparatively recently.

The fossil record of two orders of herbivorous marine mammals, the Sirenia and Desmostylia, also indicate a late Cenozoic radiation of the kelps. We summarize the evidence for this mainly from Domning's (1978) monograph on the North Pacific sirenians, except where otherwise noted.

Sirenians are known from the Early Eocene; dugongid sirenians have been distributed pantropically from the Eocene to Recent. One lineage of the family Dugongidae gave rise to Steller's sea cow (*Hydrodamalis gigas*) in the cool waters of the North Pacific. This lineage originated in the tropical Pacific during the Early Eocene with the passage of two forms (*Dioplotherium* and *Dusisiren*) from the Caribbean to the Pacific through the Panamic Portal. Both were tropical herbivores and probably fed largely or exclusively on seagrasses, in much the same way as present-day dugongs (*Dugong dugong*). The desmostylians also were widely distributed through the Pacific in the Miocene (Mitchell and Repenning 1963).

Dioplotherium and the desmostylians were extinct in the Pacific by the Late Miocene, probably because of the dwindling supply of tropical seagrasses brought about by the onset of late Tertiary cooling. *Dusisiren jordani*, also

TABLE 1. Geographical distribution of Laminariales.

	Number of species		
	North Pacific	North Atlantic	Southern Oceans
Family Chordaceae			
Chorda†*	1	1	0
Family Laminariaceae			
Agarum†*	2	1	0
Anthrothamnus#	1	0	0
Costaria†	2	0	0
Cymathere†*	1	0	0
Hedophyllum†	2	0	0
Kjellmaniella#	1	0	0
Laminaria+	14–32	5–12	4
Phyllaria†	0	1	0
Pleurophycus†*	1	0	0
Streptophyllum#	1	0	0
Thalassiophyllum†*	1	0	0
Family Lessoniaceae			
Dictyoneuropsis†*	1	0	0
Dictyoneurum†*	1	0	0
Lessonia††	1	0	3
Lessoniopsis†*	1	0	0
Macrocystis†**	2–3	0	1–2
Nereocystis†*	1	0	0
*Pelagophycus**	2	0	0
Postelsia†*	1	0	0
Family Alariaceae			
Alaria##	14	3	0
Ecklonia#++	3	0	2–3
Eckloniopsis#	1	0	0
*Egregia**	2	0	0
Eisenia†*	3	0	0
Pterygophora†*	1	0	0
Undaria#	3	0	0
Number of species	64–83	11–18	10–12
Number of genera	26	5	4

References:
† Dawson (1966).
* Druehl (1970).
# Segawa (1974).
+ Kain (1979).
†† Fritsch (1965).
** M. Foster (pers. comm.).
Widdowson (1971).
++ Chihara (1970).

a tropical/subtropical form, gave rise to *D. dewana* by the Middle to Upper Miocene in the northwest Pacific (Shizuo et al. 1986), which in turn gave rise to *Hydrodamalis* by about the mid-Pliocene. *Dusisiren dewana* is an important link between the tropical and temperate hydrodamaline dugongids. Its reduced dentition and claw-like flippers seem to be modifications associated with a transition from foraging on seagrasses to benthic algae. *Hydrodamalis* was widely distributed in the North Pacific through the late Pleistocene, and on the basis of Steller's (1751) observations it probably fed exclusively on kelp.

This scenario involving herbivorous marine mammals parallels that described earlier for limpet associates of marine macrophytes. In each case, the appearance of seagrasses and their associated herbivores in the fossil record predates the appearance of herbivores associated with kelp. We suggest that the appearance of herbivores which fed largely or exclusively on kelp reflects the emergence of kelp as an abundant resource in coastal marine systems, and thus we infer a relatively recent origin, or at least diversification, for the kelps.

Geographical distribution of kelp.—Evidence summarized in the preceeding sections suggests that the kelps proliferated and diversified in association with a polar cooling trend late in the Cenozoic. Based on their present distributions, each of the three major kelp families shows clear Pacific affinities (Table 1). All but one of 27 presently recognized kelp genera occur in the North Pacific, 19 of these exclusively. In contrast, the North Atlantic and the cool seas of the southern hemisphere (hereafter termed "southern oceans") contain only five and four kelp genera, respectively. For species-rich genera with interoceanic distributions, such as *Laminaria* and *Alaria*, the same pattern is evident at the species level (Widdowson 1971; Kain 1979). This pattern is most consistent with a North Pacific center of radiation, especially because Cenozoic climatic regimes in the northern and southern hemispheres probably were not dissimilar (Flint 1971; Savin et al. 1975; Frakes 1979), thus making it difficult to imagine why large-scale extinctions of a cosmopolitan kelp flora should have occurred elsewhere in the world.

"Center of origin" explanations for various taxa, based on gradients in diversity, have been criticized by vicariance biogeographers (Nelson and Platnick 1980, 1981; Nelson and Rosen 1981; Wiley 1981). However, differences in kelp diversity among different temperate regions are striking, and they are difficult to reconcile with alternative explanations for the diversification of the Laminariales.

Lacking a fossil record for the kelps, their routes of dispersal are best indicated by extant distributions. Some groups apparently dispersed from the North Pacific through Bering Strait and the Arctic Ocean into the North Atlantic. Others dispersed across the tropics into the southern oceans.

An early route of kelp dispersal to or from the Pacific, through the Tethyan Seaway or the Panamic Portal, when these avenues were open early in the Cenozoic, requires that the kelps are much older than we propose, and cold-water floras were able to tolerate prolonged tropical conditions. None of the modern-day kelps occur in warm, tropical seas which form an effective barrier against interhemispheric dispersal of cool water forms (Womersley 1981). Gaines and Lubchenco (1982) pointed out that fleshy macroalgae in general are inconspicuous in tropical and subtropical reef habitats. They argue that the main cause of this inconspicuousness is high intensities of herbivory (mainly by herbivorous fishes), interactions which Steneck (1983) believes have been important in marine systems since the Mesozoic.

Connections between North Pacific and North Atlantic floras must have been via Bering Strait and the Arctic Ocean and thus could not have occurred prior to the first submergence of Beringia in the Late Miocene or Early Pliocene (Hopkins 1967). Most northward kelp dispersals through Bering Strait probably occurred in the Late Pliocene or Pleistocene, based on the fossil record of marine invertebrates (Durham and MacNeil 1967). This proposed Pacific origin, and subsequent dispersal to the North Atlantic, apparently produced similar patterns of distribution and diversity in the kelps and the invertebrates. For example, in the genus *Strongylocentrotus* (Strongylocentrotidae; Echinoidea) there are (or have been) nine North Pacific species, only two of which (*S. droebachiensis* and *S. pallidus*) are known from the North Atlantic.

Kelp dispersal into the southern hemisphere probably occurred during periods of Pleistocene cooling, when the tropics were greatly compressed. Two routes across the tropics are suggested. One is via the eastern Pacific. Closure of the Panamic Portal about 5 Ma (Repenning et al. 1979) interrupted the westerly flow of tropical surface water, creating cool, nutrient-rich surface conditions in the eastern tropical Pacific. This likely facilitated dispersal of the kelps across the tropics and into the southern oceans, much as it apparently did for the otariid pinnipeds (Repenning et al. 1979). A second route may have occurred in the western Atlantic, where the clear, nutrient-poor water, typical of western tropical seas, permitted adequate light to penetrate below the thermocline, thus providing conditions suitable for kelps. The occurrence of *Laminaria* in deep water off Brazil, and its restricted distribution in the southern oceans to the west coast of Africa (Kain 1979), is consistent with this avenue of dispersal.

To summarize, although there is virtually no fossil record of the kelps, distributional patterns of the extant flora, paleoclimatological trends, and the fossil record of kelp associates suggest that kelps radiated late in the Cenozoic from a North Pacific center of origin. Are there reasonable alternatives to this suggestion, and if so, what evidence exists for or against them? In general, the alternatives are that the kelps are older than we propose, and/or they arose elsewhere. If the kelps are much older than we propose, they likely were rare. Otherwise older kelp associates should be found in the fossil record. The appearance of saddle-shaped limpets late in the Cenozoic is difficult to reconcile with this alternative. For the kelps to have diversified somewhere other than the North Pacific requires selective regional extinctions. If they had a tropical origin, the ancestral forms must have been rather different from any extant species, judging by the order's modern-day absence from warm seas. If the kelps diversified in some other temperate region, then they dispersed *en masse* to the North Pacific, and the surviving floras in those regions lost all unique taxa above the species level. Although we cannot discount these possibilities, lacking evidence, they seem unlikely.

Echinoids and benthic-feeding marine mammals

A fossil record exists for many echinoderms and molluscs because of their calcareous exoskeletons. Within these groups, most northern hemisphere taxa with cold-water affinities are thought to have arisen in the Pacific and subsequently dispersed into the Atlantic (Durham and MacNeil 1967; G. J. Vermeij, pers. comm.). Strongylocentrotid echinoids have occurred in the North Pacific since the Miocene (Smith 1984) and in the North Atlantic since the Pliocene. They are unknown in the southern hemisphere.

Two groups of benthic-foraging marine mammals are known from the late Cenozoic. One, the odobenid pinnipeds, achieved greatest diversity in the Miocene. Many species, especially dusignathine odobenids, apparently were adapted to shallow-water, benthic foraging and are thought by Repenning (1976b) to have been ecologically similar to modern-day sea otters. The dusignathines were restricted to the North Pacific and became extinct in the Early Pliocene.

Sea otters, the second group, gave rise to two lineages (Berta and Morgan 1986). One led to the extinct *Enhydriodon*; the other to the extinct *Enhydritherium* and the extant *Enhydra*. These forms were large compared with living lutrine carnivores, and all had well-developed bunodont dentition for crushing the exoskeletons of their invertebrate prey. *Enhydriodon* is known from the Miocene and Pliocene of Eurasia and Africa (Falconer 1868; Pilgrim 1931; Stromer 1931; Hendey 1978). *Enhydritherium* is known from the Late Miocene of Europe and the Late Miocene/mid-Pliocene of North America and is thought to have given rise to *Enhydra* in North America (Berta and Morgan 1986). This lineage probably originated in the Old World and apparently occurred in both the North Atlantic and Pacific regions by the late Pliocene.

There are two records of *Enhydra* from the early Pleistocene (Leffler 1964; Repenning 1976a), and one dated as Late Pliocene/Early Pleistocene (Mitchell 1966), although Repenning (1976a) suggested an early Pleistocene date for this specimen. One extinct species, *E. macrodonta* (Kilmer 1972), has been described from the late Pleistocene of California. *Enhydra* is unknown outside the North Pacific (Repenning 1976a).

These records lead us to conclude that, since at least the Miocene, a potential existed for ecological interactions between predatory marine mammals and herbivorous echinoids as they presently occur in the North Pacific Ocean.

Biological Interactions in North Pacific Kelp Forests

Our focus here will be on a specific but important set of the many ecological processes known to occur within kelp forests (Dayton 1985b; Foster and Schiel 1985; Harrold and Pearse in press)—namely, the interactions among predatory sea otters, herbivorous sea urchins, and macroalgae. We also focus on one particular region, the cool temperate/boreal North Pacific Ocean, which we loosely define as the rim of the Pacific from about the United States/Canada border to the northern Japanese archipelago. We list a number of properties of the system or its species and describe how they interact. Next, we integrate this information into a model describing how the system works. In the final sections, this model will be central to our arguments on co-evolution of plant/herbivore interactions resulting from herbivory gradients within systems, among regions, and over geologic time.

Structure of kelp assemblages

There are two locations where sea otter populations are at or near equilibrium density and where sublittoral assemblages of invertebrates and algae have been described in detail—Amchitka Island in the western Aleutian archipelago (Estes et al. 1978), and Urup Island in the southern Kurile archipelago (Shitikov and Lukin 1971). Two notable features of epibenthic plant assemblages are reported from both areas. First, most brown algal biomass is contributed by two kelp genera, *Laminaria* and *Agarum*, which comprise an estimated 80 percent and 13 percent respectively of the total biomass at Amchitka Island (Estes et al. 1978). Second, *Laminaria* and *Agarum* occupy depth-related zones. *Laminaria* spp. typically occur from Mean Low Water to depths of 12–15 m, and *Agarum* spp. occur between about 12 and 20 m depth. Similar depth patterns are reported by Yamada (1980)

(Hokkaido), Neushul (1967) (Washington State), Lamb and Zimmerman (1964) (Massachusetts) and Himmelman (1984) (Newfoundland). Thus, we believe the depth pattern to be typical of physically similar areas at which *Laminaria* and *Agarum* co-occur in the Pacific and Atlantic oceans.

Predator/herbivore interactions

The sea otter's ability to limit populations of herbivorous sea urchins is well known (McLean 1962; Lowry and Pearse 1973; Estes and Palmisano 1974; Duggins 1980; Breen et al. 1982). Two patterns of variation in the abundance and size of sea urchins are related to sea otter predation. First, sea urchins are sparsely distributed (usually rare and always inconspicuous) and usually small (<30–35 mm test diameter) in areas populated by sea otters. In contrast, sea urchins are comparatively large (<70–80 mm test diameter) and abundant in areas lacking sea otters. Benthic communities in the absence of otters are perhaps best described as mosaics of "sea urchin barrens" (*sensu* Pearse et al. 1970; Lawrence 1975; Duggins 1983) and assemblages dominated by fleshy macroalgae. The spatial pattern of these mosaics varies considerably, from instances in which the patches comprise many hectares to cases in which they are 1 m^2 or less in size (Foster and Schiel 1988). The extent (in a quantitative sense) to which sea urchin barrens constitute benthic communities in areas without sea otters is poorly known, due to logistic difficulties in making large-scale descriptions of the sea floor. Sea urchin barrens were estimated to occupy roughly 40–50 percent of the rocky benthos at San Nicolas Island, in the southern California Bight (U.S. Fish and Wildlife Service 1987), and they seem to be increasingly common at higher latitudes (J. A. Estes and D. O. Duggins, unpubl.). However, urchin barrens rarely occur in shallow water (<10–15 m depth) in areas abundantly populated with sea otters. Thus, the probability of a plant settling and growing in an area where it will be damaged or destroyed by sea urchin grazing is high in areas lacking sea otters, but virtually zero where otters are abundant. This pattern of variation in the intensity of herbivory between areas with and without sea otters is probably recent, having developed in the North Pacific following human exploitation of the species.

A second and less well-known pattern is that sea urchin density and size increase with depth where sea otters are abundant (Estes et al. 1978: Aleutian Islands; Shitikov and Lukin 1971: Kurile Islands). Two lines of reasoning indicate that this is a consequence of reduced foraging efficiency by sea otters in deep water. First, sea otters infrequently dive to depths beyond 20 to 30 m (Kenyon 1969; Estes et al. 1981) or remain submerged on a foraging dive for more than 100 seconds (Estes et al. 1981). Typical dive times and depths probably are determined by the species's aerobic dive limit (Kooyman et al. 1980, 1981). Hence, the deeper the dive, the greater the time cost in swimming from the surface to the bottom and back again. For example, about 65 percent of the time spent underwater would be expended in swimming to and from the surface during a 60-second dive (the average foraging dive time: Estes et al. 1981) to a depth of 20 m, based on an average swim rate of 1 m/sec (T. Williams, unpubl. data). Second, where sea otters are absent, the density and average size of sea urchins are greatest at the sublittoral fringe and decline with increasing depth (Estes et al. 1978). That opposite depth-related patterns of sea urchin size and density correlate with the presence or absence of sea otters supports the proposed mechanism of depth-related variation, as opposed to the alternatives that these patterns are caused by physical factors or behavioral preferences on the part of sea urchins. Increasing density and size of urchins with depth probably co-occurred in the North Pacific with diving mammals through the late Cenozoic.

Plant/herbivore interactions

Because sea urchin herbivory is an important disturbance to many kelp forest plants (Lawrence 1975; Lubchenco and Gaines 1981; Harrold and Pearse in press), variation in the intensity of herbivory should have important consequences to those plants. In the following section we discuss some of those consequences.

Brown algal phenolics.—Chemical defenses against herbivores are well known in terrestrial plants (e.g. Rosenthal and Janzen 1979; Denno and McClure 1983). Marine algae also possess many kinds of unusual "secondary" metabolites (Faulkner 1984), and there is increasing evidence that some of these metabolites act as defenses against herbivores (Geiselman and McConnell 1981; Targett and McConnell 1982; Norris and Fenical 1982; Paul and Fenical 1983; Hay 1984b; Steinberg 1985; Hay et al. 1985; Targett et al. 1986).

Phenolic compounds, in particular polyphloroglucinols (compounds resulting from the polymerization of phloroglucinol [1,3,5-trihydroxybenzene]), are among the most notable classes of defensive compounds in brown algae and are probably the most important chemical defenses in kelps. This conclusion is based on the following evidence: (1) all species of brown algae probably produce phloroglucinol and its polymers (Ragan 1976; Glombitza 1977; Ragan and Craigie 1978; Ragan and Glombitza 1986); (2) purified polyphenolics extracted from fucoid or laminarian algae, as well as polyphenolics from terrestrial plants, inhibit feeding by herbivorous marine gastropods and echinoids (Geiselman and McConnell 1981; Steinberg 1985, in press, unpub. data); (3) variation in phenolic concentration among species of brown algae (from five orders), individuals within species, and tissues within individuals are correlated with feeding preferences of marine herbivores (Anderson and Velimirov 1982; Steinberg 1984, 1985; Johnson and Mann 1986); (4) phloroglucinol and its polymers are the only likely deterrent compounds so far reported from the kelps, and they are often present in large quantities (up to 10 to 15 percent of the dry weight of some species [Katayama 1951; Steinberg 1985 and unpubl. data]); (5) polyphenolics are widespread deterrents to herbivores in terrestrial plants (Swain 1979). These findings do not exclude possible alternative functions for phenolic compounds, such as deterrence against microbes and fouling organisms, or allelopathy.

There is further evidence for the general importance of phenolics as deterrents to herbivores in the North Pacific. Steinberg (1985) reported a high correlation between phenolic concentrations in 19 species of brown algae and feeding preferences of 20 species of their common herbivores. Among the plants, species of *Laminaria* had low phenolic levels (0.23–0.49 percent dry weight; also see Geiselman and McConnell 1981; Johnson and Mann 1986) whereas *Agarum cribrosum* had comparably high phenolic levels (4.05–5.53 percent dry weight). Consumption rate studies done in sea urchin barrens at Attu Island showed that tissue from *Laminaria* spp. was consumed at almost twice the rate of *Agarum cribrosum* (J. A. Estes, unpubl. data). These data are consistent with the results of other studies in North America showing that *Agarum* is less palatable than *Laminaria* to several species of sea urchins (Vadas 1977; Larsen et al. 1980).

Consequences to herbivores.—The preceding observations demonstrate that *Agarum* more capably resists herbivory than does *Laminaria.* Although the various possible reasons for this (i.e. differences in toughness, nutrient content, secondary metabolites) have not all been evaluated, available evidence suggests that the superior defense ability of *Agarum* results from deterrent effects of its higher phenolic concentrations.

Elevated polyphenolic levels in *Agarum* also appear to have a negative effect on the fitness of echinoids. Vadas (1977), working in the San Juan Islands, Washington, demonstrated that sea urchins fed *Agarum* had substantially lower absorption efficiencies, lower growth rates, and depressed gonadal development compared with individuals fed *Laminaria.* Similar results have been obtained in the Aleutian Islands (Mayer 1980) and the northeast Atlantic (Larson et al. 1980).

Competitive interactions between Laminaria *and* Agarum.—Dayton (1975) used removal experiments to demonstrate competitive hierarchies among the most common brown algal species at Amchitka Island. Three of his results apply here. First, selective removal of *Laminaria* spp. caused a significant increase in density and percent cover of *Agarum cribrosum,* compared with unmanipulated control plots. Second, the converse experiment (i.e. selective removal of *Agarum*) caused no significant change in density or cover of *Lami-*

naria spp. Third, removal of the *Laminaria* spp. canopy from a strip through the depth gradient within which *Agarum* occurred produced a striking increase in *Agarum* cover at the shallow end of the strip. Before the *Laminaria* canopy was removed, *Agarum* cover increased with depth, from near zero at about 7 m to almost 100 percent at 18 m. These results indicate that *Laminaria* spp. are competitively dominant over *Agarum*, and at the shallow end of its depth distribution, *Agarum* is limited by this interaction.

The cost of defense.—Production of high phenolic levels in *Agarum* may constitute a physiological "cost," leading to decreased competitive ability. This is a reasonable expectation since all brown algae seem to possess the machinery for phenolic production; no biosynthetic innovation should be required for the production of phenolics by a given species (Glombitza 1977; Ragan and Craigie 1978). If high phenolic concentrations could be achieved at no substantial cost, one must reconcile why they do not occur more widely in view of the apparent advantage they offer against herbivory. The assumption is commonly made that chemical defenses in plants are costly. This assumption is fundamental to several recent theories regarding the evolution and ecology of terrestrial plant/herbivore systems (Feeny 1976; Rhoades and Cates 1976; Coley et al. 1985). Rhoades (1979: pp. 61–63) and McKey (1979: pp. 14–15) have summarized some of the evidence supporting this view.

In marine plant/herbivore systems, and within functional groups (*sensu* Steneck and Watling 1982), trade-offs between competitive ability and herbivore defenses also are often assumed to exist—a view supported by the finding that feeding preferences generally are consistent with competitive rankings of algae (Vadas 1968; Paine and Vadas 1969b; Lubchenco 1978). Although the mechanisms accounting for feeding preferences and competitive ability are poorly known, available data suggest that such trade-offs commonly occur (Lubchenco and Gaines 1981; Hay 1984b). Cost arguments also imply that different tissues within a single plant should be differentially defended against herbivores (McKey 1979). Steinberg (1984) and Johnson and Mann (1986) provide support for this hypothesis for two species of kelp.

We conclude that the biosynthesis of phenolic compounds probably involves a cost to the algae. This conclusion is consistent with the broader theoretical view of plant/herbivore interactions in marine and terrestrial systems.

Interactions among Sea Otters, Sea Urchins and Kelp: a Synthesis

We now propose a model to explain zonation between *Laminaria* and *Agarum* in the North Pacific Ocean (Fig. 1) that operates in the following way. The system is driven by the pervasive influence of sea otter predation. Because they must breath-hold to dive, sea otters incur time or energy costs in moving between the ocean's surface and the sea floor. Consequently, they are increasingly less efficient foragers in deeper water, resulting in increased sizes and densities of sea urchins in deeper water with consequent increases in the intensity of herbivory. A depth-related herbivory gradient, in turn, contributes to the zonation of kelp, with *Laminaria* and *Agarum* occurring in shallow and deep water respectively. This is because *Laminaria* is competitively superior to *Agarum*, whereas *Agarum* more effectively defends itself against echinoid herbivores. By this mechanism, *Agarum* is excluded from shallower water despite the fact that it is capable of living there, as demonstrated by Vadas (1968) and I. Yamada (personal communication), who report that *A. cribrosum* inhabits tide pools. The limiting resource in competition between *Laminaria* and *Agarum* is unknown, but it appears to be space or light. The physiological mechanism of competitive dominance may be differential rates of growth, since a rapidly growing species would be more likely to successfully occupy a break in the epibenthic canopy than a slower growing one. A similar mechanism may explain competitive dominance relationships among benthic algae in temperate littoral systems (Lubchenco 1980; Taylor and Hay 1984) and coral reef communities (Hay et al. 1983). Instantaneous growth rates from

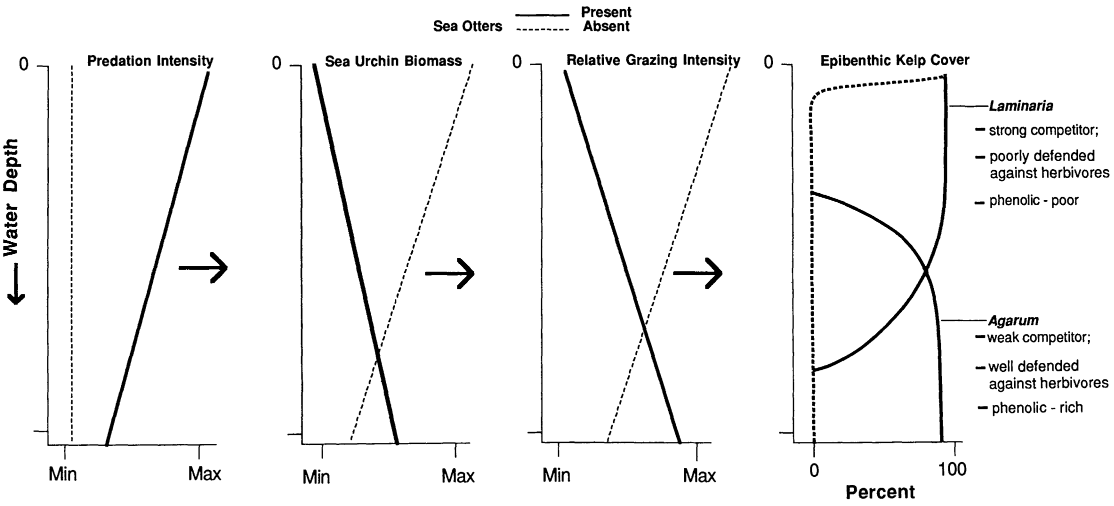

FIGURE 1. Model for the structure of epibenthic algal assemblages in the North Pacific Ocean. See text for explanation.

30 to 100 percent greater in *Laminaria* than in *Agarum* (Mann 1972) are consistent with this mechanism.

Evolution of Algal/Herbivore Interactions: a Hypothesis

The preceding historical and ecological data imply that the kelps evolved in an environment in which the intensity of herbivory in shallow water was low, due to the limiting influence of predation on sea urchins by diving mammals. In the remainder of this paper we explore this idea. We consider general differences in plant/herbivore interactions among other cool-temperate regions of the world, present likely paleohistories for important groups, and propose a hypothetical model for divergent co-evolutionary pathways between marine plants and their herbivores among the world's temperate regions.

Late Cenozoic decline of herbivory at high latitudes

There is evidence that predation (both carnivory and herbivory) has changed over geologic time. Vermeij et al. (1981), for instance, demonstrated that the frequency of molluscan shell damage and repair increased abruptly during the Mesozoic. Subsequent changes in shell architecture among warm-water faunas are thought to be adaptations against the sudden appearance of crushing predators. Vermeij (1977) termed this period of change the "Mesozoic Marine Revolution." Steneck (1983) proposed similar ideas for marine plant/herbivore interactions. On the basis of increased wounding in fossil solenopores and a trend of increased grazing in the major herbivore groups (most notably bony fishes, echinoids, and molluscs), Steneck argued that herbivory has escalated from the mid-Mesozoic to the present. He further suggested that stands of large (kelp-like) fleshy macrophytes dominated benthic communities worldwide for much of the Phanerozoic, but that these declined with the Mesozoic rise in grazing intensity.

Since relatively warm climates prevailed through most of the early and mid-Cenozoic, even around the polar margins of continents, most shallow marine provinces at that time probably were not unlike modern tropical and subtropical communities. If so, marine floras must have lacked the large fleshy algae which now are so conspicuous along the shores of cold seas. The development of large fleshy algae probably was inhibited by intense herbivory, most notably that from teleost fishes, just as today these herbivores inhibit the development of fleshy algae on hard substrates at low latitudes (Hay 1981, 1984b; Gaines and Lubchenco 1982). Successful algal species probably were well defended against herbivory by calcification, crustose or turfy life forms, and secondary chemicals (Norris and Fenical 1982; Paul and Hay 1986).

In the Late Miocene there began a gradual polar cooling trend, probably resulting in the reduction or absence of herbivorous fishes from high latitudes (Bakus 1969; Gaines and Lubchenco 1982) and thus a decline in the intensity of herbivory in these areas. We propose that these events marked the onset of a diversification and proliferation of the kelps and perhaps other groups of algae. Furthermore, since the developing temperate regions were largely isolated from one another, the evolution of plant/herbivore interactions may have varied among these regions. For instance, the northern and southern hemispheres were isolated by the tropics; the North Pacific and Atlantic Oceans by North America and Eurasia; the south temperate zones by broad expanses of deep water. In the following sections we examine the similarities and differences among some of these regions.

The predators: invertebrates, fish, reptiles, birds, and mammals

Predatory marine invertebrates are a diverse group, with broad influence. Vermeij (1978) argued that crushing predators have had an important influence on the evolution of invertebrate shell form in tropical marine systems, but that at higher latitudes these effects are much less. K. Mann and associates (Mann 1973; Breen and Mann 1976) have claimed that the American lobster (*Homarus americanus*) was responsible for limiting populations of herbivorous sea urchins in the northwest Atlantic until lobsters were recently reduced by human exploitation, although Pringle et al. (1982) and Miller (1985) disputed this claim. Crabs may limit urchins in the eastern North Atlantic (Muntz et al. 1965). Asteroids in the North Pacific probably limit herbivorous molluscs and echinoids under some circumstances (Harrold 1982; Duggins 1983). Yet in no instance has the widespread importance of predation by invertebrates on herbivorous molluscs and echinoderms in temperate waters been demonstrated.

Benthic-feeding fishes prey on and limit populations of herbivorous invertebrates from tropical (Hay 1984a) to warm temperate areas (Andrew and Choat 1982; Cowen 1983). However, the importance of fish predation appears to decline with increasing latitude, becoming virtually insignificant in cool temperate waters (Palmer 1979). Thus, benthic-feeding fishes probably have been comparatively unimportant predators of herbivorous echinoids and molluscs at high latitudes during the late Cenozoic.

Marine reptiles are largely tropical in distribution, and most are herbivores or pelagic feeders. Marine turtles, some of which range into high latitudes, have been severely reduced throughout the world by hunting, net entanglement, and the disturbance or destruction of nesting beaches. However, there is no evidence that marine reptiles limited herbivorous benthic invertebrates in temperate waters at any time during the late Cenozoic.

Various shorebird species limit populations of some intertidal invertebrates (O'Connor and Brown 1977; Hartwick 1981; Frank 1982; Hockey and Branch 1984; Botton 1984; Marsh 1986). Several species of diving ducks feed on molluscs and echinoids, but there are no documented cases of important predator/prey interactions between diving marine birds and herbivorous benthic invertebrates. Extant bird species appear ill-equipped, both morphologically and behaviorally, for feeding on large invertebrates, and the fossil record provides no indication of extinct diving birds with morphological adaptations to crush the shells or tests of large molluscs and echinoids (Olson 1985).

From what is known of modern sea otters, benthic feeding mammals may have a nearly ubiquitous limiting influence on many of their prey, particularly echinoids. We conclude from this brief review that no predator group in cool-temperate seas is comparable to the benthic feeding mammals in their ability to limit herbivorous invertebrate populations. During the late Cenozoic, such mammals were important only in the northern hemisphere, and especially in the North Pacific. Benthic-feeding species in these taxa never inhabited the southern hemisphere. The South American marine otter (*Lutra felina*) occurs in temperate coastal waters of Chile and Peru, and although there has been speculation of a convergence in ecological function with *Enhydra*, that is surely not true. *Lutra felina*, like its congeners, is essentially a piscivore, with none of the behavioral or morphological characters possessed by *Enhydra* for feeding on benthic invertebrates (Castilla 1981; Sielfeld 1983; Riedman and Estes 1988).

Otariid pinnipeds dispersed to the southern hemisphere in the Pliocene/Pleistocene, after they were completely developed as piscivores (Repenning et al. 1979). Phocid pinnipeds, which now are common around both polar ice caps, apparently have been piscivorous since their tethyan or paratethyan origin (Repenning et al. 1979).

Thus, there is no evidence that benthic-feeding marine mammals occurred in the southern hemisphere, at least late in the Cenozoic. In the northern hemisphere, however, if dusignathine odobenids and late Miocene/Pliocene sea otters were even closely comparable in predatory function to modern sea otters, it seems likely that low-density populations of herbivorous echinoids and molluscs characterized shallow seas.

Plant/herbivore interactions

Our ecological model (Fig. 1) predicts that with decreasing intensities of predation, there should be an escalation in herbivory, to which the plants should respond by increasing their defenses against herbivores at the expense of decreased competitive ability. From this model, and the historic and geographic information presented earlier, we hypothesize the following. Kelp species evolved (1) recently, (2) in the North Pacific Ocean, and (3) in an environment in which the intensity of herbivory was low because of the limiting predatory influences of sea otters, their ancestors, and perhaps dusignathine odobenids. This resulted in weakly coevolved plant/herbivore interactions. That is, there was little selective pressure for plants to evolve defenses against herbivores, or for herbivores to respond to those defenses. In contrast, neither sea otters nor dusignathine odobenids occurred in the southern hemisphere, where predators of comparable influence apparently are lacking now and were lacking in the past.

Populations of herbivorous echinoids, therefore, may not have been limited by predation in the temperate southern hemisphere over geologic time. If so, herbivores should have been abundant; the intensity of herbivory on algae should have been great; and more tightly coupled plant/herbivore interactions may have evolved. We expect the plants to have developed more substantive chemical defenses in response to more abundant herbivores, and the herbivores, in turn, to have developed improved capacities to tolerate plant defenses.

Are these predictions supported by the evidence? Many seem to be, although there are exceptions.

Community-level patterns.—Patch mosaics between sea urchin barrens and algal-dominated assemblages occur in many temperate regions. They have been reported from the western North Atlantic by Mann (1972, 1977), Fletcher et al. (1974), Arnold (1976), Hooper (1980), Himmelman (1980), Trembley and Chapman (1980), and Whitman et al. (1982); the eastern North Atlantic by Kain (1977), and Norton (1978); South America by Dayton (1985a); South Africa by Fricke (1979); New Zealand by Ayling (1981), Andrew and Choat (1982), Choat and Schiel (1982), and Schiel (1982); and southeastern Australia by Fletcher (1987), Fletcher and Underwood (1987), and Steinberg (unpubl.). The proportion of rocky habitat consisting of urchin barrens in these regions is unknown, although Harrold and Pearse (in press) suggest that urchin barrens occur more widely in the northern than the southern hemisphere.

The distribution of phenolic-rich species.—Phenolic levels are low but variable among the common species of brown algae in the North Pacific (Steinberg 1985). Most species are phenolic-poor, a few are phenolic-rich, and most individual plants are poorly defended against herbivores. From the herbivores' perspective, there is a choice in food quality as far as phenolic levels are concerned.

The distribution of phenolic-rich species in the southern oceans is more poorly known. Our model predicts that they should be common. South America and South Africa have depauperate brown algal floras. Furthermore, except for the work of Anderson and Velimirov (1982), secondary compounds in these species, and the feeding preferences of their herbivores, are unstudied. Thus, our subsequent focus is on northern New Zealand and southeastern Australia, where more work has been done.

Common species of fucoid algae in temperate Australia and New Zealand often contain 10–15 percent (by dry weight) total phenolics (Steinberg, in press, unpub. data). This is two to three times the levels found in phenolic-rich species from the northeastern Pacific (Steinberg 1985). Furthermore, the most common and widely distributed kelp species in Australia and New Zealand, *Ecklonia radiata,* is rich (4–12 percent) in phenolics. Some of these species also contain other, potentially defensive, secondary metabolites such as terpenes and hydroquinones (Faulkner 1984). Australian fucoids, such as *Cystophora* and related genera, seem particularly rich in these metabolites (Ravi et al. 1982; Gregson et al. 1977; Kazlauskas et al. 1980, 1981), although they are unknown from fucoids in the northeastern Pacific.

Herbivore feeding preferences.—Molluscan and echinoid herbivores in the North Pacific prefer to feed on brown algal species with low phenolic levels (Steinberg 1985). Invertebrate herbivores in the southern hemisphere should be less sensitive to variation in phenolic levels. That is, if a high proportion of plant species and individuals are well defended chemically, then selection pressures on their herbivores to adapt to these defenses should also have been greater than they were in the North Pacific. Schiel's (1982) finding that several fucoid algae in New Zealand are high-preference species of the herbivorous echinoid *Evechinus chloroticus* is consistent with this prediction, as are our preliminary experimental results from northern New Zealand and two sites in southern Australia (Steinberg, unpubl.). The diets of several species of herbivorous fishes in Australia and New Zealand [*Odax pullus* (Clements 1985), *Kyphosus sydneyanus* (Russell 1970; Steinberg, unpubl. data), and *Olisthops cyanomelas* (S. Shepherd and P. Steinberg, unpubl. data)] also are largely comprised of phenolic-rich algae, suggesting a level of tolerance to these compounds. This contrasts with northeastern Pacific herbivores, such as *Medialuna californiensis* and *Girella nigricans,* which appear to feed on phenolic-poor kelps (Quast 1968).

We reiterate that the larger view put forth in this paper is a hypothetical evolutionary model, not a fact or a conclusion. As such, further tests are necessary. We urge that further studies be done with the predictions of this model in mind. The following questions are addressable, and their answers would be very illuminating. Do phenolic compounds function exclusively in herbivore deterrence, or do they serve other important purposes as well? Are marine algae in the southern hemisphere generally better defended against herbivores than those in the North Pacific? Are southern hemisphere herbivores less selective feeders than those in the North Pacific? Is predation on benthic invertebrates generally less important in the southern hemisphere than it is in the North Pacific? To what extent is interspecific competition important in southern hemisphere algal assemblages? Will future fossil discoveries or other paleontological findings prove consistent with our claims? As is true for many hypothetical models, this one has no simple test. Its ultimate truth likely will come through the careful formulation of specific predictions and a collective view of information from the tests.

Conclusions

In summary, we propose that the kelps radiated in the North Pacific Ocean late in the Cenozoic, during which time plant/herbivore interactions were not unlike those that occur presently in many areas. Our bases for this proposition are that (1) spatial variation in the intensity of herbivory by sea urchins in cold-temperate and boreal systems is largely driven by the influence of sea otter predation, and (2) sea urchins, sea otters, and other benthic feeding marine mammals have occupied the northern hemisphere since at least the Late Miocene. Temperate coastal regions of the southern hemisphere apparently lacked predators of comparable influence during this same period of earth history. A likely result was variation among habitats in the intensity of herbivory when cold-water floras were evolving. This variation in the intensity of herbivory may have selected for different qualities in plants occupying the different habitats.

The observed patterns lend support to our hypothesis, but as largely *a posteriori* observations, they do not constitute legitimate tests. Although we believe the evidence is definitive that phenolic compounds deter certain herbivores, this does not establish that phenolic-rich floras evolved through exposure to intense herbivory. An alternative hypothesis is that plants in physiologically stressful environments, such as might be expected under low light levels or suboptimum nutrient regimes, must better defend themselves against herbivores than must plants in benign environments (Coley et al. 1985). As yet, we have only looked at the common brown algae. If predictable differences in the intensity of herbivory have occurred among habitats, and if these differences were responsible for selecting the observed patterns in secondary chemistry as defenses against herbivores, then we would expect to find qualitatively similar patterns in other floral elements among these same habitats. Comparative studies of herbivore resistance in the red algae could provide independent tests of the hypothesis. Conversely, if the stressful environment hypothesis is correct, we should expect to find abiotic environmental factors more highly correlated with patterns of herbivore defense than are differences among habitats in the intensity of herbivory.

Patterns in the spatial dynamics of predation, herbivory, and plant defenses against herbivory, similar to those suggested here, have been reported in other aquatic systems. Spatially predictable variation in herbivory, caused by varying probabilities of predation on the herbivores, may influence plant distribution in such varied systems as prairie streams (Power and Mathews 1983), tropical reefs (Ogden et al. 1973; Hay 1981, 1984a), and temperate rocky intertidal communities (Hockey and Branch 1984). Furthermore, among coral reef habitats, Hay (1984b) has found plant defenses against herbivores to be correlated with intensities of herbivory from grazing fishes. Although further study is needed to determine if such patterns occur more widely, the fact that they are known from several different systems makes our hypothesis plausible.

The near extinction of sea otters that occurred during the past two centuries was a major disturbance to coastal biological communities in the North Pacific region. We imagine that shallow-water kelps were suddenly exposed to intensities of herbivory that they could not withstand, thus perhaps explaining the devastating effects of sea urchins on many kelp forests in the northern hemisphere.

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