Response to Domning

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Domning's critique of our essay on kelp evolution (Estes and Steinberg 1988) makes 2 main points: that the kelps (Order Laminariales) radiated earlier, and perhaps much earlier, than our suggested late Cenozoic date; and that herbivorous marine mammals (desmostylians and sirenians) probably exerted an important selective influence on the kelps which is ignored in our evolutionary scenario. We respond to each point in turn.

When did the kelps radiate?

We argue that the kelps "radiated" extensively after the onset of late Cenozoic cooling (presumably sometime following the Middle to Late Miocene). The limited distribution of all extant kelp species to cool seas, a clear geographic affinity of the kelps to the North Pacific, and the established timing of paleoclimatic changes in this area led us to conclude that the kelps, as we now know them, must be rather young. We make no claims about the time of "origin" of the Laminariales, or of higher level taxa within the Order. Domning's alternative to our view is based largely on the Middle Miocene fossil kelp *Julescraneia*. It seems a very bold step to conclude on the basis of two specimens of this single species that the Lessoniaceae were well differentiated by the Middle Miocene, and that much of the adaptive radiation of the kelps must have preceded this time. The distinguishing characters of the Order Laminariales are tissue differentiation in the thalli into epidermis, cortex, and medulla (Abbott and Hollenberg 1976), yet Parker and Dawson (1965: p. 274) state in their published description of *Julescraneia* that the specimens ". . . lack all traces of their original tissues." Fleshy macroalgae are notorious for their highly plastic morphologies, yet Parker and Dawson's assignment of *Julescraneia* to the Laminariales and Lessoniaceae is based entirely on external morphology. Although we have not examined the actual specimens, the plate published by Parker and Dawson adds further doubt in our own minds to the assignment of this material.

More recent evidence for the timing of kelp evolution is provided by Fain et al.'s conclusion (1988: p. 299) that ". . . the similar values of (chloroplast DNA) percent sequence divergence observed within kelp and angiosperm families may indicate that species lineages within the Laminariales are similar in age to those within the Leguminosae." Since the angiosperms arose and diversified late in the Mesozoic (Knoll 1987) this finding demonstrates that Domning's view is plausible. It does not, however, resolve the question of when the extant kelps *radiated*. Since the angiosperms are much younger than the earliest algae whereas algal chloroplast genomes appear to be evolving at higher rates than those of land plants (Palmer 1987), existing molecular evidence does not exclude a comparatively recent radiation and diversification of the kelps. Further work in plant molecular genetics should help resolve this issue.

We also note that our hypothesis for a late Cenozoic radiation of the kelps does not really conflict with Steneck's (1983) hypothesis for a much earlier origin of kelp-like fleshy algae, as Domning implies. Steneck suggested that large fleshy algae abounded in the Paleozoic prior to the Mesozoic escalation of grazing by teleost and invertebrate herbivores. We do not argue this point, but would argue that any such plants probably were not kelps. The distinction is an important one as there are several groups of large fleshy marine algae besides the kelps, e.g., certain rhodophytes, chlorophytes, and several other orders of phaeophytes, in particular the Desmarestiales, Dictyotales, and Fucales. Some of these groups, including other phaeo-

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phytes, probably arose much earlier than our proposed timing for the radiation of kelps (Fry and Banks 1955; Bold and Wynne 1978; Clayton 1984).

Domning acknowledges that the warm marine conditions which prevailed across the Pacific rim until late in the Cenozoic are problematic for the exclusively cold-adapted kelps, and goes on to suggest that the "... kelps might have survived from the cooler Oligocene in small, peripheral, cool-water refuges, possibly the Bering Sea or the Sea of Okhotsk." Although many possibilities can be imagined, this explanation seems to us to be rather contrived. We are aware of no evidence that major cold water refuges persisted through the Miocene south of Beringia. Any such refuges must have been large and physically diverse to contain even a moderate proportion of the extant kelp species. We can better imagine such areas existing north of Beringia in the Arctic Ocean. However, the problem with this latter scenario is that an early Arctic Ocean flora would have had free access to disperse into the North Atlantic, in which case all but a small subset of the diverse Arctic Ocean/North Atlantic kelp flora went extinct after inoculating the North Pacific following the opening of Bering Strait during the Late Miocene or Pliocene. The more likely scenario, in our view, is that like many marine invertebrates (Durham and MacNeil 1967), the kelps originated in the North Pacific and dispersed through Bering Strait into the Arctic and North Atlantic oceans in the Late Pliocene or Pleistocene.

Was kelp evolution influenced by the desmostylians and sirenians?

Domning argues that herbivorous marine mammals must have exerted important selective influences on kelps and other fleshy macroalgae. While this is an intriguing hypothesis, there is no real evidence to support or refute it. A fundamental difficulty, of course, is that since the hydrodamalines and desmostylians are extinct, most aspects of their biology and ecology probably will remain forever unknown. Thus, it may never be possible to unravel their role as herbivores in the North Pacific Ocean.

Of these two groups of herbivorous marine mammals, Domning apparently favors the desmostylians as being the more important in kelp evolution, largely because they occupied high latitudes in the North Pacific during the Late Oligocene temperature minimum. Unfortunately, in contrast with Steller's sea cow (*Hydrodamalis gigas*) which clearly fed on marine algae, by Domning's own admission the evidence is insufficient to judge whether the desmostylians fed on marine algae or angiosperms. A more serious problem is that the desmostylians were extinct by the Late Miocene, and thus absent from the putative arena of kelp evolution throughout the period of late Cenozoic polar cooling. The desmostylians could not possibly have exerted any influence on marine plants for at least the last 10 m.y.

Judging from their dental morphology and Steller's direct observations of *Hydrodamalis gigas*, the hydrodamaline sirenians were probably algal feeders. In addition, *H. gigas* probably was abundant over much of the North Pacific rim until it was exterminated by early hunters. Domning's earlier work makes these points convincingly, and although they are not sufficient to demonstrate the importance of hydrodamalines as algal herbivores, they are necessary.

Our main difficulty with Domning's argument is that the observed characteristics of kelp forest ecosystems run counter to what one would expect had kelp evolution been strongly influenced by marine mammal grazing. Domning has pointed out here and in his earlier papers that *H. gigas* probably was unable to dive. If true, its grazing influence would have been limited largely or exclusively to surface canopy species and those that live in the littoral zones or at the sublittoral fringe. The inability to dive would have effectively disassociated these herbivores from the epibenthic kelps—thus disassociating them from most kelp species and most habitats presently occupied by kelps.

However, grazing by *H. gigas* may indeed have had an important influence on species of kelps in the surface canopy and at the sublittoral fringe. It is interesting to note that all of the surface canopy-forming kelp species, with the exception of giant kelp (*Macrocystis* spp.) are annuals which appear to be competitively subordinate to the epibenthic kelps (Dayton 1975; Duggins 1980), and that two of these surface canopy species (*Macrocystis* spp. and *Alaria fistulosa*) bear their reproductive tissues near the holdfast whereas most of the epibenthic kelps distribute their reproductive tissues throughout their blades (Estes et al. in press). Furthermore, the sublittoral fringe over much of the central and western North Pacific is dominated by *Laminaria longipes*, a peculiar kelp species because it propagates vegetatively via a rhizoid-like holdfast, which permits it to reoccupy space rapidly following disturbances. It is appealing to imagine these life history characteristics as adaptations to sea cow grazing. Unfortunately, the habitats where *Hydrodamalis* presumably foraged are also those that are most strongly influenced by physical disturbances from ocean waves. Thus, physical disturbance effects are a reasonable and likely alternative to the hypothesis that the evolution of these life history characteristics were influenced by marine mammal grazers. This alternative is further supported by the fact that all of the surface canopy-forming kelps and *L. longipes* are poorly defended by secondary chemicals (Steinberg 1985, 1989), since chemical defenses could affectively deter disturbances by herbivores but would have no influence on physical disturbances.

We have pointed out (Estes and Steinberg 1988; Steinberg 1989) that most of the kelps contain low concentrations of phlorotannins as well as other potentially deterrent secondary compounds. If Domning is correct in arguing that kelp evolution was influenced by herbivorous marine mammals, our findings can only be reconciled by assuming that the secondary chemicals that kelps were capable of producing were not deterrent to these animals. Large terrestrial mammals are often deterred or otherwise affected by phenolics (Robbins et al. 1987a,b), as are birds which feed on salt marsh angiosperms (Buchsbaum et al. 1984). Thus, algal polyphenolics seem to have the potential to affect herbivorous marine mammals, and if these mammals were important kelp grazers one would have expected the kelps to have invested more heavily in chemical defenses. Secondary chemicals, of course, are not the only way in which marine algae defend themselves against herbivores, but secondary compounds seem to be an especially common means of deterring herbivory in marine systems (Hay and Fenical 1988).

If the kelps did not respond to herbivorous marine mammals by increased production of polyphenolics, how then did these mammals influence kelp evolution? This important question is left unanswered by Domning's scenario. From our knowledge of the extant kelp flora, species that are good competitors and poorly defended are found precisely where the influence of herbivorous mammals should have been the strongest, which is to say, in shallow water. At best, this is a paradox. In contrast, our proposed scenario involving diving carnivores and herbivorous invertebrates is consistent with observed patterns of variation in competitive versus defense abilities of the kelps and their analogues on several spatial scales.

In sum, we acknowledge that our proposed scenario is speculative, and that herbivorous marine mammals may have influenced the organization of kelp forest ecosystems and even the evolution of kelp species. However, the mere fact that these herbivorous mammals existed is insufficient evidence to infer any such ecological and evolutionary effects. Although Domning offers an intriguing alternative scenario, we believe it presents too many inconsistencies with our present knowledge of the kelps, kelp forest ecosystems, and plant/herbivore interactions.

Literature Cited

ABBOTT, I. A., AND G. J. HOLLENBERG. 1976. Marine Algae of California. Stanford University Press; Stanford.

BOLD, H. C., AND M. J. WYNNE. 1978. Introduction to the Algae. Prentice Hall; Englewood Cliffs, New Jersey.

BUCHSBAUM, R. N., I. VALIELA, AND T. SWAIN. 1984. The effect of phenolic compounds and other plant constituents on feeding by Canada geese in a coastal marsh. Oecologia *63*:343–349.

CLAYTON, M. N. 1984. Evolution of the Phaeophyta with particular reference to the Fucales. Progress in Phycological Research *3*:11–46.

DAYTON, P. K. 1975. Experimental studies of algal canopy interactions in a sea otter-dominated community at Amchitka Island, Alaska. Fishery Bulletin *73*:230–237.

DUGGINS, D. O. 1980. Kelp beds and sea otters: an experimental approach. Ecology *61*:447–453.

DURHAM, J. W., AND F. S. MACNEIL. 1967. Cenozoic migrations of marine invertebrates through the Bering Strait region. Pp. 326–349. *In* Hopkins, D. M. (ed.), The Bering Land Bridge. Stanford University Press; Stanford.

ESTES, J. A., D. O. DUGGINS, AND G. B. RATHBUN. In press. The ecology of extinctions in kelp forest communities. Conservation Biology.

ESTES, J. A., AND P. D. STEINBERG. 1988. Predation, herbivory, and kelp evolution. Paleobiology *14*:19–36.

FAIN, S. R., L. D. DRUEHL, AND D. L. BAILLIE. 1988. Repeat and single copy sequences are differentially conserved in the evolution of kelp chloroplast DNA. Journal of Phycology *24*:292–302.

FRY, W. L., AND H. P. BANKS. 1955. Three new genera of algae from the upper Devonian of New York. Journal of Paleontology *29*:37–44.

HAY, M. E., AND W. FENICAL. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. Annual Review of Ecology and Systematics *19*:111–145.

KNOLL, A. H. 1987. Patterns of change in plant communities through geological time. Pp. 126–141. *In* J. Diamond and T. J. Chase (eds.), Community Ecology. Harper and Row; New York.

PALMER, J. D. 1987. Chloroplast DNA evolution and biosystematic uses of chloroplast DNA variation. American Naturalist *130* (Supplement):S6–S29.

PARKER, B. C., AND E. Y. DAWSON. 1965. Non-calcareous marine algae from California Miocene deposits. Nova Hedwigia *10*: 273–295.

ROBBINS, C. T., T. A. HANLEY, A. E. HAGERMAN, O. HJELJORD, D. L. BAKER, C. C. SCHWARTZ, AND W. W. MAUTZ. 1987a. Role of tannins in defending plants against ruminants: reduction of protein availability. Ecology *68*:98–107.

ROBBINS, C. T., S. MOLE, A. E. HAGERMAN, AND T. A. HANLEY. 1987b. Role of tannins in defending plants against ruminants: reduction in dry matter digestion. Ecology *68*:1606–1615.

STEINBERG, P. D. 1985. Feeding preferences of *Tegula funebralis* and chemical defenses of marine brown algae. Ecological Monographs *55*:333–349.

STEINBERG, P. D. 1989. Biogeographical variation in brown algal polyphenolics and other secondary metabolites: comparison between temperate Australasia and North America. Oecologia *78*:373–382.

STENECK, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. Paleobiology *9*:44–61.