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AMPHIPODS ARE NOT ALL CREATED EQUAL: A REPLY TO BELL

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In laboratory feeding trials, Hay et al. (1987) found that the tube-building amphipod *Ampithoe longimana* readily consumed the brown seaweed *Dictyota dichotoma,* which was not eaten by local fish. The diterpene alcohols pachydictyol A and dictyol E, which are produced by this species of *Dictyota,* significantly deterred feeding by fish but either stimulated or did not affect feeding by the amphipod. Based on these data, Hay et al. (1987) suggested that small, relatively sedentary mesograzers like the amphipod they studied might experience decreased predation if they lived on seaweeds that were chemically defended and thus not commonly consumed or visited by omnivorous or herbivorous fishes. Because predation is a major source of mortality for amphipods and other mesograzers (see references in Hay et al. 1987), they reasoned that selection might favor sedentary mesograzers that could live on and eat chemically defended seaweeds.

Their idea was tested more broadly by applying the same reasoning to a tube-building polychaete in North Carolina (Hay et al. 1988*b*), a nontube-building but macrophyte-inhabiting amphipod in the Caribbean (Hay et al. 1988*a*), a specialist Caribbean amphipod that eats and lives in a mobile domicile it builds from a chemically defended species of *Dictyota* (Hay et al. 1990), and crabs and ascoglossans in the Caribbean and tropical Pacific that live and feed only on certain chemically defended seaweeds (Hay et al. 1989, Hay, *in press*). In each of these cases, the mesograzers were unaffected or stimulated by compounds that deterred feeding by herbivorous or predatory fishes. Only the ascoglossans deterred predation using metabolically sequestered algal defenses. The other mesograzers tested were not distasteful to predators, but were found to avoid detection or ingestion due to their close physical association with the defended algae. This association protected the mesograzers from carnivorous as well as herbivorous fishes (Hay et al. 1989, 1990).

Bell (1991) takes issue with the interpretation of the initial study of Hay et al. (1987). She contends: (1) that amphipods rarely, if ever, eat macroalgae in the field and that results of laboratory feeding assays conducted by Hay et al. may have been artifacts of not having presented amphipods with appropriate alternative foods; (2) that because amphipods are rarely feeding specialists and may eat epiphytes while living on larger seaweeds, a strong relationship between plant secondary compounds and amphipod feeding is unlikely to be established, and (3) that suggesting a functional

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equivalency of amphipods to insects may not be pragmatic. We consider each of these potential problems below. Although the ideas developed by Hay et al. (1987) have proven useful when applied to numerous other mesograzers (see review by Hay, *in press,* or the references above), Bell's comments focus specifically on amphipods, and we shall also emphasize these mesograzers.

Do Amphipods Eat Macroalgae?

Hay et al. (1987), Bell (1991), and others have generalized about amphipods as a group without adequate appreciation for the great variance in feeding preferences and other behaviors that exist among the >5000 species of amphipods. Many of our apparent disagreements with Bell may arise from failure to recognize this diversity. Hay et al. (1987: 1578) noted that epiphytic microalgae were important foods for many, if not most, species of amphipods. We thus agree with Bell on this point. However, we strongly disagree with the contention that the particular species studied by Hay et al. (1987), as well as several other species, do not graze macroalgae under field conditions.

Tegner and Dayton (1987, also see Dayton and Tegner, *in press*) provide an unusual but impressive example of what certain herbivorous amphipods can do to macrophytes if the amphipods escape control by their consumers. Following the El Niño event of 1982–1984, amphipod populations (primarily *Ampithoe humeralis*) increased dramatically, apparently due to a short-term decrease in abundance of predatory fishes. Within a 6-mo period when kelps are usually growing at their maximal rates, the amphipod reduced the area of kelp canopy along that part of the California coastline from 632 to 275 ha. Some areas were completely denuded of all macroalgae except the encrusting corallines (Dayton and Tegner, *in press*). A similar event appears to have occurred >20 yr earlier (Jones 1965). The disturbance caused by El Niño is a recurring but rare perturbation to this system; although this type of dramatic damage to macroalgae is rare, it clearly shows that some amphipods can, and occasionally do, severely affect seaweed populations. The failure of such amphipod species regularly to affect macroalgal population dynamics may have more to do with the activity of amphipod consumers than with the inability of these amphipod species to consume seaweeds.

The potentially diverse and species-specific effects of amphipods on large seaweeds and their epiphytes are illustrated by a recent mesocosm experiment (Duffy 1990). The large brown seaweed *Sargassum filipendula* was placed in outdoor tanks with natural flowing seawater, and allowed to develop a heavy cover of fouling material consisting primarily of diatoms, the filamentous alga *Ectocarpus siliculosus,* and detritus. When the amphipod *Caprella penantis* was placed in replicate tanks, its feeding significantly reduced the epiphyte load, but had no significant effect on the host seaweed. In contrast, the amphipod *Ampithoe marcuzii* had no effect on epiphyte load but preferentially consumed *Sargassum.* Over a 10-d period, *Sargassum* plants exposed to *A. marcuzii* decreased in biomass by 11% despite an abundant supply of epiphytes and detritus; the biomass of *Caprella*-stocked plants and of amphipod-free control plants increased by 95 and 81%, respectively, during the same period (Duffy 1990). Earlier studies also documented large differences among species in what amphipods eat and in their utilization of microalgae vs. macrophytes (Caine 1977, Zimmerman et al. 1979, Brawley and Fei 1987).

Bell states that "data to examine macroalgal versus epiphyte availability and ingestion by amphipods under field conditions are rare." We agree, but would add that adequately controlled and replicated studies in the field are not only rare, they are nonexistent. For the present, we must therefore rely on less direct evidence such as macroalgae in the guts or feces of field-collected amphipods (Glynn 1965, Martin 1966, Moore 1977, D'Antonio 1985, Gunnill 1985) or the consumption of macroalgae in the laboratory while epiphytic algae are also available (Zimmerman et al. 1979, Brawley and Fei 1987, Hay et al. 1987, Duffy 1990). It is unclear to us why some investigators who have documented consumption of both microalgae and macroalgae by amphipods assumed that the data on microalgal grazing were real and that those on macrophyte grazing derived from experimental artifacts (D'Antonio 1985, Brawley and Fei 1987). Rigorous data allowing an assessment of potential artifacts are unavailable for these studies. Although we find the authors' arguments plausible, there is at present no clear way of distinguishing what is and is not artifact in such laboratory feeding assays, and we see no reason why half the data should be accepted and the other half rejected.

Keeping in mind that data from laboratory assays and gut contents are constrained by potential artifacts and errors of interpretation, the available data from both field observations and laboratory experiments are consistent. They indicate that some species of amphipods consume primarily microalgae and detritus, while other species eat macrophytes as well as the smaller algae (Zimmerman et al. 1979, Brawley and Fei 1987, Hay et al. 1987, Duffy 1990).

We stress that the diversity in amphipod feeding (and other behaviors) precludes most broad generalizations about the ecology of this taxonomic group. The fact that some amphipods, or even most amphipods, do not eat macroalgae does not mean that no amphipods do so. The rare but dramatic effects of amphipod grazing on kelp-bed seaweeds, the presence of macroalgae

in the guts and feces of field-collected amphipods, the resistance of several macrophyte-inhabiting amphipods to seaweed chemical defenses, and the common occurrence of amphipod grazing scars on numerous species of seaweeds from a wide variety of habitats (Norton and Benson 1983, Buschmann and Santelices 1987; J. E. Duffy and M. E. Hay, *personal observation*) convince us that some species of amphipods commonly graze macrophytes. The relative importance of amphipod grazing on microalgae vs. macrophytes in undisturbed field situations is unknown.

In summary, we believe that the diversity of viewpoints on amphipod feeding reflects, at least in part, the variation among species in their feeding habits. We do not argue that most amphipods eat macroalgae, only that the distinction between those that do and those that do not is important, and has possible consequences regarding selection for amphipod resistance to seaweed chemical defenses and for comparisons of marine mesograzers with terrestrial herbivores.

Must Amphipods Be Specialists to Develop Resistance to Chemical Defenses?

We think not. Bell's question regarding the degree of feeding specialization necessary to select for resistance to plant defenses is perhaps the most important one for evaluating the proposed (Hay et al. 1987) linkage between predation pressure and mesograzer diets. She asks, "if amphipods are commonly not feeding specialists on chemically defended algae, . . . would one expect a strong relationship between secondary compounds and amphipods to be established?" Bell correctly notes that *Ampithoe longimana* and most other seaweed-associated amphipods are habitat generalists, are surprisingly mobile (compared to our opinions when we wrote the earlier paper, see references in Bell 1991), and are unlikely to become highly specialized on any alga (although this has occurred in one case: Hay et al. 1990). Despite the apparent soundness of this argument, *A. longimana,* other amphipods, and numerous other mesograzers show a strikingly similar pattern of preferential feeding on seaweeds that are chemically defended from fishes (reviewed by Hay, *in press*). How can this be explained?

Fish predation is among the most pervasive selective factors affecting the biology of amphipods and other mesograzers (see references in Hay et al. 1987); in areas of high herbivore pressure, chemically defended seaweeds are often common and could provide both food and shelter for herbivorous amphipods. Because the most abundant predators of amphipods at the North Carolina study site of Hay et al. (1987) are sparid fishes that also eat seaweeds, selection might favor amphipods that could live on and eat a wide variety of seaweeds that are resistant to fish grazing. This is consistent with recent findings that *A. longimana* is unaffected by numerous seaweed metabolites that effectively deter fish feeding (Duffy 1989; M. E. Hay and J. E. Duffy, *personal observation*).

Several other recent studies of generalist mesograzers (Hay et al. 1988*a, b,* Duffy 1989) support the ideas of Hay et al. (1987) and point to an emerging pattern. These mesograzers show strong preferences for feeding on seaweeds that are chemically defended from fishes, and the mesograzers are somehow generally more resistant than fishes to the lipid-soluble metabolites produced by these seaweeds. Similar patterns of generalized resistance to plant chemical defenses have been documented for terrestrial insects that use the mixed-function oxidase (MFO) system to detoxify a diverse group of lipophilic metabolites via hydroxylation, demethylation, and epoxidation (Futuyma 1983). Such broad resistance to plant chemical defenses suggests that the amphipod studied by Hay et al. (1987) may possess an active MFO-type system that provides general resistance to lipophilic metabolites; such systems occur in many generalist insect herbivores (Futuyma 1983). This strategy would not require close evolution of amphipods with any particular plant species and is consistent with the presently available data. The ability of the amphipod studied by Hay et al. (1987), as well as other amphipods and mesograzers (see Hay, *in press*), to tolerate seaweed compounds that deter fishes suggests that they could be ecologically similar to some terrestrial insects and may rely on similar detoxifying mechanisms.

Thus we are not convinced that resistance to plant chemical defenses would be expected only from specialist herbivores having a long history of association with particular defended plants. Such a relationship does not hold for insect herbivores (Futuyma and Moreno 1988); even generalist insect herbivores encountering a novel plant with novel chemical defenses can be capable not only of resisting the plant's defenses but also of sequestering them, despite the fact that the insect and plant are native to different continents and would have had no evolutionary contact (Blum et al. 1990).

Is It Instructive to Compare Amphipods and Terrestrial Insects?

Similarities and differences between marine amphipods and insects have been discussed elsewhere (Schiel and Choat 1980, 1981, Brawley and Adey 1981, Hay and Fenical 1988, Hay et al. 1988*a, b,* 1989, 1990, Hay, *in press*), and need not be repeated in detail here. We are intrigued by the parallels and contrasts between amphipods and insects, we have learned much by attempting such comparisons, and we find the comparisons useful despite, and indeed partly because of, the

many important differences between these groups. In their 1987 paper, Hay et al. suggested that macrophyte-eating marine amphipods were similar to terrestrial insects in that they lived on the plants they ate, were subject to heavy rates of predation, and might be able to diminish this predation by associating with plants that are chemically defended from larger consumers. We still consider these similarities valid, especially since recent work suggests that terrestrial insects (Bernays 1989), amphipods, and other marine mesograzers (see Hay et al. 1990, Hay, *in press*) can all diminish predation by feeding on certain plants. Future work may resolve some of the differences in opinion on the interactions between plants, mesograzers, and their predators, and on similarities between mesograzers and insects. If our arguments are correct, we expect that (1) preferential association of mesograzers with chemically defended seaweeds should be more common in more sedentary species, for which food and habitat are more closely linked, than in more mobile species, and (2) preferential association with chemically defended plants should be more common in areas with greater intensity and/or consistency of predation pressure.

Although clear differences between marine and terrestrial herbivores exist when some characteristics are compared (Hay and Fenical 1988, Hay et al. 1990, Hay, *in press*), we find that pursuing these contrasts is both informative and useful, in that much understanding and cross-communication between marine and terrestrial investigators can be achieved in the process.

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