Marine–Terrestrial Contrasts in the Ecology of Plant Chemical Defenses Against Herbivores

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Small marine herbivores that live on the plants they consume often selectively eat seaweeds that are chemically defended from fishes. Their feeding is unaffected or stimulated by the plant metabolites that deter fishes, and these small herbivores dramatically reduce their susceptibility to predation by associating with host plants that are noxious to fishes. Ecological similarities between these small marine herbivores and numerous terrestrial insects suggest that herbivorous insects also may have evolved a preference for toxic plants because this diminishes their losses to predators, parasites and pathogens. Although marine and terrestrial plants and herbivores evolved in strikingly different environments, the ease of experimentation in some marine systems makes them ideal for addressing certain questions of fundamental importance to both terrestrial and marine workers.

Certain fundamental differences between plants and herbivores in marine and terrestrial communities must be discussed before these systems can be productively compared. Terrestrial plants allocate biomass to below-ground structures that are unavailable to many herbivores, and much of the above-ground mass may be woody structural tissue that is of little nutritional value. Because seaweeds live in a buoyant medium and take up nutrients through their photosynthetic thalli, they don't make roots or allocate as much mass to non-photosynthetic structural materials. Seaweeds are therefore all foliage, completely above ground and very available to herbivores.

On herbivore-rich portions of coral reefs, seaweeds commonly lose 1–3.5% of their total mass each day or 60–100% of their total production, with herbivorous fishes alone taking 40,000 to 156,000 bites/m²/day (Ref. 1). The most intensively grazed terrestrial systems appear to be African grasslands grazed by large herds of ungulates that move about 66% of above-ground production. Given the large allocation to below-ground structures, this may be no more than about 33% of total production, about 1/3 to 1/2 of the rates in marine communities. In both marine and terrestrial systems, herbivory is generally greater in tropical than in temperate areas, but the highest rates of herbivory on tropical coral reefs can be ten to 100 times greater than the highest rates in tropical forests.

Most herbivory in terrestrial systems is due to insects and vertebrate homeotherms. Insects are largely absent from marine systems, and most herbivory is due to vertebrate ectotherms (fishes) and a diverse array of invertebrates that are present all year and rarely undergo diapause (sea urchins, gastropods, polychaetes and a variety of marine crustaceans). Because virtually all marine herbivores are ectotherms, changes in temperature may affect herbivory rates more in marine than in terrestrial systems. With decreasing temperature, herbivory decreases in marine systems, but may increase in terrestrial communities because of the increased energy demands that low temperatures place on vertebrate homeotherms.

Terrestrial herbivores cope with the large amounts of relatively indigestible cellulose, hemicellulose and lignin that occur in terrestrial plants by (1) timing their life cycles such that the feeding stages co-occur with the seasonal flush of new, high-quality leaves; (2) sucking plant sap and thus avoiding the structural materials; and (3) harboring microbial gut symbionts that make cellulose energetically available to the herbivore. These strategies appear rare among marine herbivores, although sap sucking occurs among the ascoglossan sea slugs. These slugs feed primarily on chemically-rich green seaweeds from which they sequester both defensive secondary metabolites and functional chloroplasts. These continue to fix carbon for up to three months and pass much of this energy on to the slug. The apparent absence of cellulose-digesting microbial symbionts among most marine herbivores may be an artifact of the minimal effort marine investigators have devoted to their study.

There can also be dramatic differences between marine and terrestrial herbivores in how food quality and abundance affect basic population biology. As an example, the tremendous physiological and morphological plasticity of sea urchins results in their population density and survivorship being largely unaffected by resource levels. When algal resources decline, individual urchins shrink in size by resorbing skeletal material and differentially allocating resources to body parts used for food gathering. This allows urchins to overexploit local resources, turning kelp beds into urchin barrens, while remaining at high densities for many years thereafter, neither dying nor dispersing. This pattern contrasts with terrestrial systems where changes in plant resources appear to have large effects on the population biology of herbivores.

Reviewing this broad, conceptually rich and complex topic in a short article forces crude generalizations and mandates that intellectually intriguing subtleties and important specifics be omitted in favor of stressing selected general points. I hope this comparison stimulates communication among marine and terrestrial workers, but it cannot adequately represent the depth and richness of either field. Interested readers should therefore consult the more lengthy articles listed in the references.

Selection for plant defenses

In marine communities, most selection for plant defenses is generated by a diverse assemblage of generalist grazers consisting primarily of fishes, sea urchins and gastropods. Because these grazers are generalist feeders, they can occur at high densities relative to the abundance of their favored food plants. They often drive these to local extinction, thus having a profound effect on marine communities.

In contrast, many terrestrial workers explicitly state or assume that most herbivory is due to...
insects, most of which are relatively specialized feeders. If this apparent difference is real (but see Ref. 5 for a persuasive argument that mammalian herbivores are more important), then terrestrial plants would be under greater selection for traits that deter a limited number of specialists, and marine plants for traits that deter a broad range of taxonomically diverse generalists. Thus, the potential for closely linked coevolution between pairs of interacting species would be lower in marine than in terrestrial communities. Although there has been a long history of considering insect-plant relationships as coevolved, recent studies suggest that true coevolution is unlikely and apparently uncommon in both marine and terrestrial systems (see also Ref. 20). Coevolution of insects and plants may be less common than was once thought for several reasons, including (1) the limited impact of insect herbivores; (2) the great present-day, and possibly greater historic, effect of mammalian herbivores; and (3) the importance of physical stresses in interrupting coevolutionary processes. Interactions that appear to be coevolved often may not be. For example, encrusting coralline algae and their associated gastropod herbivores provide an exceptional fossil record of a plant-herbivore interaction. However, although the characteristics of both the plants and herbivores suggest a strong history of coevolution, the fossil record demonstrates that the major 'herbivore deterrent' characteristics of the algae evolved many millions of years before the herbivores. The supposedly coevolved characteristics of these plants and herbivores appear to be based primarily on fortuitous preadaptations rather than reciprocal evolution. Terrestrial studies show similar patterns, with some closely associated plants and insects showing little, if any, evidence of coevolution.

It is clear, nevertheless, that the prevalence of specialized herbivore species differs dramatically between marine and terrestrial systems. Insects make up the huge majority of herbivore species in terrestrial communities (herbivorous insects and the plants they eat may comprise 50% of the world's species), and it has been estimated that about 90% of herbivorous insect species feed on three or fewer families of plants. In contrast, most marine herbivores are very opportunistic, commonly feeding on ten to more than 20 families of plants and often supplementing their diets with animal material.

Some of the differences in feeding specificity between terrestrial and marine habitats could result from basic differences in life history and recruitment modes of common herbivore species. In terrestrial communities, adult insects in some speciose groups spend minimal time feeding and are often short lived, mobile, widely dispersing and equipped primarily for reproduction and careful placement of eggs on appropriate host plants. Juvenile stages are often longer lived, relatively immobile and do most of the feeding. These generalizations hold for diverse orders, such as the Lepidoptera and Diptera, but not for others, such as the Coleoptera and Hemiptera. The inconsistent and sometimes very poor correlation between the rank order of host species selected by ovipositing females and the performance of the larval stages on these hosts suggests that host specificity is often determined more by the behavior of the female than by the physiological needs of the feeding stage. For example, female Drosophila magnaquinaria normally oviposit only on skunk cabbage (Lysichiton americanum), but their larvae grow significantly better on tomato (Lycopersicum esculentum) plants.

Most marine herbivores contrast with terrestrial Lepidoptera and Diptera in that adults do most of the feeding and are usually less mobile than the juveniles. The relatively short-lived juvenile stages may move over great distances because adults liberate larvae into the plankton rather than placing them carefully on appropriate hosts. Marine herbivores, therefore, have less ability than most insects to choose the host plant onto which they will settle, because larvae are usually returned to coastal habitats by the actions of physical oceanographic processes (currents, internal waves, etc.) rather than by directional swimming. Additionally, within a habitat, approaching the bottom often entails large losses to predators. This should select against specialists that would need to approach the bottom many times in order to encounter their particular host, and for generalists that would be able to feed on whatever they encountered following settlement.

Specialist herbivores occur in marine communities, but they are uncommon and appear to have relatively minimal effect on their host plants. Regardless of the relative importance of different herbivores, it is clear that selection has favored both marine and terrestrial plants having a variety of chemical, structural or life history characteristics that diminish losses to herbivores. Focusing on the similarities and differences between plants and herbivores in marine versus terrestrial communities may provide clues to factors affecting the evolution of feeding specialization and to the ecology and evolution of plant-herbivore interactions in general.

**Effects of plant chemical defenses on herbivore feeding patterns**

Both marine and terrestrial plants produce a diversity of secondary metabolites that deter feeding by herbivores; differences occur primarily due to the near absence of alkaloid production by seaweeds and the common addition of halogens to seaweed compounds. In contrast to terrestrial studies, many experiments assessing the effectiveness of seaweed secondary metabolites have been conducted in the field (usually on relatively undisturbed coral reefs), assaying the compounds against the summed feeding of the diverse array of herbivores attacking the plant. These types of field experiment minimize the need to assume which herbivores are, or are not, important, and allow a rigorous test of specific metabolites and the selective advantage they would confer under natural conditions. Assays can then be run in the lab to assess the effects against particular herbivores. The data from these studies show that a large number of chemically diverse secondary metabolites significantly reduce plant...
Fig. 1. (a) Feeding preferences (mean ± 1 SD) of two common omnivorous fishes and two common
mesograzers, all of which co-occur in the temperate Atlantic along the southeastern coasts of the United
States. The brown seaweed *Dictyota menstrualis* (formerly *Dictyota dichotoma*) was preferred by the
mesograzers but avoided by the fishes. (b) Feeding preferences on palatable seaweeds treated (shaded)
and untreated (hatched) with two diterpene alcohols that are produced by *D. menstrualis*. The
metabolites deterred feeding by both fishes but either stimulated or did not affect feeding by the
mesograzers. Numbers in parentheses at the bases of the hatched histograms on the right give the
number of paired samples used in each assay. Data were compiled from Refs 33 and 34.

losses in both the laboratory and
the field; however, there is often
tremendous variance in the effects
of a given compound on different
herbivores and of related com-
pounds on the same herbivore.19

Such differences may also be
seen among geographic regions. For
instance, brown algal in the north
Pacific produce polyphenolics at
concentrations of 0–6% of algal dry
mass, and the palatability of these
algae to invertebrate herbivores is
broadly predictable on the basis of
polyphenolic content.27 These same
types of alga in Australia and New
Zealand produce polyphenolics at
up to three times the concentration
of those in the north Pacific. How-
ever, at these sites, polyphenolic
content is not a predictor of algal
palatability and polyphenolics that
significantly deter herbivores in the
north Pacific have little if any effect
on Australasian herbivores.28,29

There also appear to be dramatic
differences in polyphenolic produc-
tion between seaweeds in temper-
ate and tropical communities.
Polyphenolic production is common
among temperate brown algae, but
on herbivore-rich tropical reefs
where virtually all plants are 'bound
to be found' by generalist grazers,
polyphenolics are rarely produced
in significant quantities.29 This is
opposite to the pattern that would
be predicted by land-based theo-
ries1,30,31 and to the pattern seen in
comparisons of temperate and trop-
ical forests.1

There appears to be no funda-
mental difference in the effective-
ness or mode of action of tannins
versus other types of compo-
ounds.28,29,32, and there is clearly
little if any validity in assessing allo-
cation to chemical defenses by
clumping compounds into crude
categories such as total terpenes or
total phenolics. Small alterations of
chemical structure such as the lo-
cation of one hydroxyl group on a
diterpene molecule can change a
compound from a feeding deterrent
to a stimulant.1 Although terrestrial
ecologists have commonly grouped
plant secondary metabolites into
broad categories for quantification
or for discussing their general mode
of action, this now appears no
more appropriate for terrestrial than
for marine compounds.32

What selects for resistance to plant
chemical defenses?

Terrestrial ecologists debate
which factors select for resistance to
plant chemical defenses and what
role this resistance plays in the
evolution of host-plant specializa-
tion.18,19,22,23,31 Early assertions that
insects have specialized to partition
resources or to increase their meta-
bolic efficiency have been generally
discounted.13,16,22–24 Present efforts
are focused more on the role host
specialization may play in allowing
herbivores to diminish the impact of
their natural enemies, to find mates,
to identify appropriate physical
habitats and to avoid making feed-
ing mistakes that involve consuming
plant toxins; however, the relative
importance of these factors is
debated.13,15,18,21–24,31

Marine studies support the hy-
pothesis that small herbivores such
as insects and marine mesograzers
(herbivores 0.2 to 20 mm in length,
such as amphipods and small crabs)
that have limited mobility and are
subject to high potential rates of
 predation may preferentially feed
on chemically-rich plants in order to
minimize their susceptibility to
natural enemies.25,26,31,37 Figure 1
shows one example of this from the
temperate Atlantic. The com-
mon omnivorous fishes *Diplodus
holbrooki* and *Lagodon rhomboides*
both avoid feeding on the brown
alga *Dictyota menstrualis* due to its
production of diterpene alcohols
that significantly deter their feed-
ing.34,35 In contrast, the polychaete
Platynereis dumerilii and a mixed species group of amphipods (primarily Ampithoe longimanus), both of which live in nonmobile tubes that they build on the seaweeds from which they feed. Selectively consume the chemically-rich seaweed Dictyota. Feeding by these mesograzers is neither not affected or is stimulated by the same compounds that deter the fishes. By selectively living on a seaweed that is chemically defended from, and thus seldom visited by, omnivorous fishes, these small relatively sedentary herbivores appear to diminish their losses to consumers. During seasons when fishes feed most actively, abundance of Ampithoe longimanus declines on species of Dictyota that deter fishes, and in field and laboratory assays, they experience dramatically reduced fish predation when they associate with these plants21,25,26,37. This host-associated refuge works even when the attacking fishes are carnivores rather than herbivores or omnivores23,26,37.

Losses to enemies were diminished by host-specific crypsis26,37, host-specific decreases in encounter frequency25,26,37, and host-derived chemical defenses25,26,37. These same mechanisms operate to diminish the susceptibility of insects to their enemies in present-day terrestrial communities15,18,22,23, and it has been suggested that toxic plants would have been even more important refuges before the Pleistocene extinctions removed common megaherbivores (mammoths, camels, horses, etc.) from several continents1. By living on hosts that were unpalatable to megaherbivores, insect larvae may have reduced indirect consumption by these large mammals. Predator avoidance or deterrence may be a major factor selecting for both insects and marine mesograzers that feed from, or become specialists on, chemically-rich plants.

However, in marine communities, this method of minimizing predation is used by generalists as well as specialists and evolving resistance to a seaweed defensive metabolite rarely leads to specialization, even if the metabolite is selectively sequestered as a predator deterrent19. It appears that several generalist mesograzers are resistant to a broad range of unrelated lipophilic metabolites that deter fish feeding. Although these mesograzers prefer to feed from plants producing these compounds, they also continue to feed from many other unpalatable plants19.

Thus, although acquisition of 'enemy-free space' may be very important in selecting for host use in both marine mesograzers and terrestrial insects, it does not sufficiently explain the differing degrees of specialization between these groups. Both generalist insects25 and marine mesograzers10 can selectively feed on toxic plants and reap the rewards of decreased predation without becoming as specialized as is common among insects in general. The unresolved question of why insects are so commonly host-plant specialists and why this occurs so rarely among other herbivores, either terrestrial or marine, is one of the most vexing questions to arise from contrasts of marine and terrestrial systems and deserves increased attention.

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