Marine Plants and their Herbivores: Coevolutionary Myth and Precarious Mutualisms [and Discussion]

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Marine plants and their herbivores: coevolutionary myth and precarious mutualisms

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SUMMARY

Planktonic and benthic algal–herbivore interactions are reviewed. In many cases, generation times of plant and herbivore are similar, yet there is no clear example of a coevolutionary arms race. Mutualisms have evolved, but these are vulnerable to extinction. We suggest that this vulnerability is caused by the loss of evolutionary flexibility accompanying the tightly linked, coadapted gene complexes.

1. INTRODUCTION

A study of interactions among species is the classical domain of the community ecologist. In particular, the elaboration by theoretical ecologists of the logistic equation has provided an interesting insight into the dynamics of competition, exploitation (e.g. plant–herbivore, prey–predator and host–parasite interactions) and mutualism. However, when attempting to relate empirical observations from nature to predictions of ecological theory, it is important to bear in mind the evolutionary context in which the species or populations of study are contained. In this sense, the species interactions can be viewed as examples of coevolution (*sensu* Ehrlich & Raven 1964). This early definition of coevolution embraced all evolution resulting from biological interactions among species, but is now more commonly called diffuse coevolution (Futuyma & Slatkin 1983). Coevolution is more frequently reserved for stepwise, reciprocal evolution (Janzen 1980) resulting in species tracking each other's response over long periods of geological time.

(a) Some considerations from theory

The majority of ecological models of species interactions have underlying assumptions, often unstated, which can make it hazardous to extend them to include evolution. For example, continuous-time models assume that the interacting species 'perceive' time in the same way, even though their evolutionary generation times may be very different. This problem can be removed by defining r in terms of the rate of increase per unit of absolute time. The problem re-emerges, however, if the evolution of the parameter r is to be considered, as this will occur with an evolutionary timebase perhaps more related to generation time than to absolute time. Discrete-time models clearly suffer from similar problems, as the finite difference equation for each species must relate to its generation time in evolutionary models.

In general, if we consider systems of differential equations describing interacting species, unless the individual time constants are very similar, it is possible to decouple the equations and treat them as though they were independent. If there is to be some emergent property of the species interactions, it is necessary that the ratio of the evolutionary generation times of the species should approach unity (for general models of species interactions, this ratio can be defined as the number of genotypes of species A encountered by a single genotype of species B). This requirement is approximately met among a wide range of marine plants and their herbivores.

(b) Marine–terrestrial comparisons

Marine benthic and terrestrial communities are characterized by interactions among dissimilar organisms, with independent evolutionary histories involving different phylogenetic and environmental constraints. Both, however, sustain broadly similar biological interactions, which have been the subject of several incisive reviews (Hay *et al.* 1987; Hay & Fenical 1988; Pfister & Hay 1988). Most marine benthic herbivores have broad diets, whereas most terrestrial herbivores are relatively specialized. This difference may reflect the contrasted mechanisms of recruitment in the two environments. Insects constitute the majority of grazers among terrestrial communities. The adults disperse and oviposit on precisely selected host plants, which may be relatively rare and inconspicuous. Marine macroherbivores, mostly fishes, sea urchins and large molluscs, liberate planktonic larvae, dispersed passively in water currents and unable to respond to locational stimuli over anything but the shortest distances (Butman 1987). Mesoherbivores, including small crustaceans, polychaetes and snails, disperse as larvae or as adults, but in either case there is usually a large component of undirected drift. Hence, whereas insects can be sure of locating a precise target and afford to be

[55]

231

specialists, marine grazers generally cannot (Hay & Fenical 1988).

Macroherbivores have generation times similar to, or greater than most macroalgae upon which they feed and in mesoherbivores generation times are similar to, or less than those of their host algae (Hay & Fenical 1988). Generations times of marine benthic herbivores and macroalgae, therefore, are more closely matched than those of insects and flowering plants, and so might be expected to be more conducive to coevolution. For the same reason, this may also be expected of planktonic herbivores and microalgae. We shall show, however, that there is no more evidence of coevolution between herbivores and plants in aquatic than in terrestrial environments and we discuss the restrictive conditions likely to promote reciprocal evolution.

2. THE COEVOLUTIONARY MYTH

(a) Herbivory and antiherbivory

Macroalgae are important members of intertidal and shallow, subtidal, rocky habitats throughout the world, where they may contribute substantially to primary production. Much of this enters the detritus food chain (Mann 1973) and, in some situations, relatively little appears to be taken by herbivores. For example, on British coasts, dense zones of fucoids and kelp often show only sporadic signs of being heavily grazed. In contrast, tropical hard substrata are usually sparsely vegetated, but when herbivorous fish are excluded, a richer algal canopy develops (Lewis 1986). Such geographical variations suggest that macroalgae are well defended against all but the most powerful herbivores, mainly certain fishes and sea urchins. Herbivorous fishes are largely confined to warmer seas (Horn 1989), whereas sea urchins extend also into cold-temperature regions where they may exert strong grazing pressure subtidally (Vadas 1990). A few specialized gastropods also damage macroalgae (Hughes 1986), but snails are usually relatively mild grazers. Increasing evidence, however, reveals that small mesoherbivores, including isopods, amphipods, crabs, polychaetes and snails, consume far more macroalgal tissue than previously suspected (Brawley 1991). Clearly, grazers pose a general threat to macroalgae, which show a variety of defences. Among these defences, secondary metabolites are of renowned importance.

Like terrestrial vegetation, seaweeds produce a spectrum of secondary metabolites including terpenes, aromatic compounds and polyphenolics. Unlike terrestrial plants, seaweeds often incorporate halogens into these compounds and, being nitrogen limited, do not produce alkaloids (Hay & Fenical 1988). Rhodophytes widely produce aliphatic halo-ketones, brominated phenols and terpenes. Chlorophytes are typified by ephemeral, undefended species, but the order Caulerpales contains perennial species producing terpenoids. Phaeophytes produce polyphenolics, differing from those in terrestrial plants in being derived from phloroglucinol, hence the term 'phlorotannins' used for these compounds. Whereas the secondary metabolites of red and green algae are lipophilic and can be applied via organic solvents to the surface of otherwise palatable plants, the phlorotannins are water soluble and must be immobilized in agar for presentation to herbivores. Feeding trials using these techniques have abundantly shown that many secondary metabolites deter herbivores (Hay & Fenical 1988).

However, despite burgeoning data showing that particular secondary metabolites repel grazers (Hay & Fenical 1988), repellency is not predictable from molecular structure. Compounds that deter one species may have no effect on another (Steinberg 1988) and seemingly trivial changes in molecular arrangement may prove to be critical. Dictyol-B and dictyol-E differ only in the position of one hydroxyl group, yet the former deters grazing by the rabbitfish *Siganus doliatus*, whereas the latter does not (Hay 1991; Hay *et al.* 1988a). Repellent algae, however, mainly produce a range of secondary metabolites, resulting in a general effectiveness against macroherbivores. Overall, the picture is one of defence on a broad front, not of reciprocal, one-to-one combat between macroalgae and macroherbivores.

Less widespread in the phytoplankton than among benthic macroalgae, toxicity is a property of certain freshwater cyanobacteria and marine dinoflagellates. Planktonic cyanobacteria and algal protists have generation times in the order of 0.08–4.1 days (Fogg & Thake 1987). They are eaten by zooplanktonic cohabitants, including ciliates, rotifers, crustaceans and pelagic tunicates, which have generation times of some 0.5–30 days (Fenchel 1974; Allan 1976). Because the ranges of generation time are displaced only by an order of magnitude, the zooplanktonic populations closely track the phytoplanktonic and therefore are usually the principal source of plant mortality (Steele 1974). Not surprisingly, phytoplanktonic species often have attributes, including unmanageable dimensions, undigestibility and toxicity, that reduce vulnerability to the zooplankton (Porter 1977).

Toxicity can be effective against passively filtering cladocerans which temporarily cease feeding. The response, however, is variable; lake *Daphnia* respond quickly to *Microcystis*, whereas pond *Daphnia*, normally living in the absence of this toxic species, respond more slowly and consequently suffer greater mortality (DeMott *et al.* 1991).

Toxicity, however, is particularly appropriate against raptorial feeders, as these generally are more sensitive to food quality (Porter 1977). Raptorially feeding copepods grasp individual particles and although several items may accumulate in the mouth parts to be handled simultaneously (Vanderploeg *et al.* 1990), the individual nature of initial capture makes it feasible to select or reject items by their nutritional quality or toxicity. *Diaptomus birgei* rejects live *Microcystis aeruginosa* but consumes dead clumps that presumably have lost their toxicity (DeMott & Moxter 1991).

In the marine phytoplankton, toxicity is the hallmark of certain dinoflagellates. Unlike endotoxic freshwater cyanobacteria, these dinoflagellates secrete

exotoxins, whose concentration in the seawater may reach dangerous proportions for copepods. *Calanus pacificus* grows poorly through its non-feeding, naupliar stages and suffers greater mortality when in the presence of toxic *Phytodiscus brevis* or *Gonyaulax grindleyi* (Huntley *et al.* 1987). In subsequent feeding stages *C. pacificus* discriminates against *G. grindleyi*, but a small proportion of cells may accidentally be ingested. Regurgitation, after a lag of some 45–120 min, minimizes the impact of the toxins (Sykes & Huntley 1987).

The effect of dinoflagellate toxins on marine copepods is similar to that of cyanobacterial toxins on freshwater cladocerans. Feeding rates are depressed and the secondary effects of starvation, reduced growth rate and lowered fecundity alleviate grazing pressure at the population level. This is enforced more acutely when exotoxins directly reduce growth and survivorship of naupliar stages. Together, these factors add positive feedback when hydrographical conditions favour growth of the dinoflagellate populations and so may contribute to the formation of blooms (Huntley *et al.* 1986).

As with the chemical defences of macroalgae, phytoplanktonic toxins are unpredictable in their effects. One toxin may affect certain grazers and not others, and a given grazer may be inhibited by some toxins and not others (Gilbert 1990). Apart from the weak correlation between sensitivity of *Daphnia* to toxic cyanobacteria and incidence of these bacteria in the habitat (DeMott *et al.* 1991; Gilbert 1990), there is no evidence of any evolutionary counter-response of zooplankters to the threat of poisoning.

(b) *Sequestering defences*

Macroherbivores are usually highly mobile, covering relatively large distances over which they may encounter a wide variety of algae. Here, there is scope for selective feeding during each foraging bout, when unpalatable algae may be avoided. Mesoherbivores, by contrast, are far less mobile and often the food plant is also their home and habitat. If this plant is unpalatable to macroherbivores, especially fishes, the associated mesoherbivores will be less at risk to predation than they would on an unprotected plant. Accordingly, mesoherbivores tend to exploit algae that are repellent to macroherbivores, so gaining 'enemy-free space' (Price *et al.* 1980).

Unless they become exceptionally numerous, mesoherbivores do not seriously damage their host algae, being kept far below carrying capacity by predators (Nelson 1979; Stoner 1980; Carpenter 1986). It is not surprising, therefore, that algae fail to produce secondary metabolites effective against mesoherbivores. Dictyol-E and pachydictyol-A repel herbivorous fish and urchins, but not the amphipod *Amphithoe longimana* or the polychaete *Platynereis dumerilii*, both of which prefer chemically defended algae such as *Dictyota dichotoma* and *Sargassum filipendula* (Hay *et al.* 1988*b*). Indeed, secondary metabolites repelling macroherbivores may become specifically attractive to mesoherbivores.

The Caribbean amphipod *Pseudamphithoides incurvaria* specializes on chemically defended algae such as *Dictyota bartayresii*. Not only does the amphipod use these algae for food and shelter, but also cuts out pieces to construct a portable case in which to live (Hay *et al.* 1990). *P. incurvaria* is reluctant to use algae, even species of *Dictyota*, lacking diterpenes that repel herbivorous fish. Moreover, when presented with the normally palatable chlorophyte, *Ulva* spp., treated with differing concentrations of pachydictyol-A, *P. incurvaria* responds more readily to higher dosages, but when forced to build domiciles from untreated *Ulva*, the amphipod becomes vulnerable to fish predation.

Metabolic sequestering of secondary compounds occurs in a number of opisthobranchs, including the sea hare, *Aplysia californica*, which accumulates toxins from its food plants, *Laurencia* spp. and *Plocamium* spp., so gaining protection from predators (Stallard & Faulkner 1974). The most specialized feeders of all, however, are the ascoglossans. These sea slugs lance plant cells and suck out the sap. Each species specializes on algae with a particular morphology. The radular tooth forms a precision tool, suited to the shape and size of algal cell to be pierced, and in those slugs feeding on filamentous algae, the foot, likewise is moulded to the dimensions of the filament (Jensen 1983).

Ascoglossans are predominantly green, owing to the chloroplasts they have ingested, sequestered and maintained in diverticulae of the digestive gland (Clark & Busacca 1978). Photosynthates of the chloroplasts are an important resource for the slugs, whose dorsal flaps and frills increase the light-capturing surface area (Hughes 1986).

When feeding on chemically defended algae, ascoglossans sequester secondary metabolites, in addition to chloroplasts. *Elysia halimedae* selects the young, diterpenoid-rich, growing edges of its host plant, *Halimeda macroloba* (Paul & Van Alstyne 1988). When attacked, the slug secretes a repellent mucus, containing a sequestered and slightly modified diterpenoid that deters fish.

The sequestering of secondary metabolites seems not to be a round of coevolution in favour of the mesoherbivores, but the specialized exploitation of resources that happen to be a ubiquitous, permanent feature of the habitat. The resources themselves appeared as an evolutionary response of the host algae to a completely different set of grazers, the macroherbivores.

We conclude that among diverse taxa of aquatic herbivores and plants, offensive and defensive strategies have evolved not in reciprocal escalation, but as parallel responses to selection pressures associated with the general problems of eating (Horn 1989) and being eaten (Norton & Manley 1990). History and phylogeny will have played important roles in shaping these responses.

(c) *The fossil record*

Inferences about coevolution, based on present circumstances, usually are severely weakened by a lack of evidence from the past. Fortunately, there is an

exception among marine plant–herbivore interactions. Calcareous, encrusting algae fossilize well and sometimes bear grazing marks clearly attributable to particular herbivores, also well represented as fossils. If there has been any stepwise, reciprocal evolution between these plants and their herbivores, it should be evident from the geological record (Steneck 1983, 1986, 1991).

Encrusting coralline algae, cosmopolitan occupants of hard substrata in shallow seas, are grazed by herbivores able to excavate the armoured thalli. Even such powerful grazers cannot normally inflict fatal damage and encrusting corallines typically predominate in areas of high grazing intensity. Armoured defence is achieved at the cost of slower growth (Steneck 1985) and greater susceptibility to fouling (Paine & Vadas 1969). Consequently, many encrusting corallines depend on grazers to prevent competitive exclusion and smothering (Steneck 1983).

In temperate regions, urchins and limpets graze the encrusting corallines. Limpets sometimes have become specifically associated with host plants (Estes & Steinberg 1988), probably because they use the host as habitat in addition to food. The wide-mouthed shell requires a close fit to the substratum if dislodgement by predators or water movement is to be resisted effectively (Hahn & Denny 1989). In the North Atlantic, *Tectura testudinalis* has a mutualistic relationship with the thick, encrusting coralline *Clathromorphum circumscriptum*, in which the limpet gains greater resistance to predators and the coralline is kept clear of fouling organisms (Steneck 1982). Are the defensive properties of corallines, the excavating ability of limpets and mutualism the result of stepwise, reciprocal evolution?

Encrusting algae resembling corallines originated in the Precambrian (Grant *et al.* 1991), before any herbivores had yet appeared. The first coralline to be morphologically differentiated, as in modern species, was *Archaeolithophyllum*. It possessed cellular fusion, a basal hypothallus, inner meristem and outer epithallus, and conceptacles enclosing spores and gametes. In the late Carboniferous, *Archaeolithophyllum* formed banks in moderately turbulent, shallow reef environments. The curly, discoidal thalli grew freely on sediments and were never cemented to hard substrata, as modern forms usually are. The suite of characters listed, enabled *Archaeolithophyllum* to recover from abrasion and breakage, caused by waves in stormy weather, but would become equally important among other corallines, millions of years later, in surviving damage inflicted by excavating herbivores.

Cellular fusion had evolved suddenly. It provided a mechanism for translocation, upon which differentiation into non-photosynthetic parts would depend, so paving the way for a radiation which even now may not yet have reached its limit. Key features in this radiation have been the potential for rapid lateral growth, an ability to encrust hard substrata, architectural diversity of the thallus, protection of spores and gametes within conceptacles and the capacity to regenerate tissues lost by deep wounding (Steneck 1983).

Despite possession of these characters by *Archaeo-*

lithophyllum in the Palaeozoic, radiation of the encrusting corallines only gathered momentum some 100 million years later, towards the end of the Jurassic (Steneck 1983). Before the radiation, corallines had occupied sediments, and their fossils bear no grazing marks. Powerful, excavating herbivores were absent at that time and hard substrata were monopolized by fleshy algae, competitively superior to the corallines.

Limpets, urchins and herbivorous fishes, all powerful excavators, radiated in the Middle Mesozoic and early Cainozoic. They stripped the fleshy algae from hard substrata and tipped the competitive balance in favour of the encrusting corallines, whose own radiation ensued. 'True' limpets appeared in the late Triassic, preceding the radiation of encrusting corallines. They began to diversity in the Jurassic, but their grazing marks are found on the shells of bivalves and ammonites, where the limpets probably were feeding on epiphytes and endophytes. By the Cainozoic, limpet grazing marks also became relatively common on encrusting corallines (Steneck 1983).

The geological record, then, shows a sequence of independent evolutionary events. First, the evolution of translocation and morphological differentiation in encrusting corallines. This was selectively advantageous in turbulent, abrasive sedimentary habitats. Second, the evolution of deeply grazing limpets, urchins and fishes. This cleared fleshy algae from rocks and opened up a new habitat for the encrusting corallines, whose abrasion-resistant thalli and high regenerative capacity pre-adapted them to survive herbivory. Meanwhile, another major taxon of calcareous encrusting algae, the Solenoporaceae, lacking such pre-adaptations, became extinct (Steneck 1983). Neither the grazing mechanisms of the herbivores nor the principal resistive mechanisms of the coralline algae evolved in relation to each other.

During the extensive radiation of the encrusting corallines and coincidental radiation of herbivores, there was opportunity for some evolutionary 'fine tuning', in which the herbivores became more powerful, while the algae became morphologically less diverse and more resistant (Steneck 1986). Included in the fine tuning, were mutualisms such as that between *Clathromorphum circumscriptum* and *Tectura testudinalis*.

C. circumscriptum has an exceptionally thick, multilayered epithallus that sustains grazing by *T. testudinalis*, yet protects the deeply underlying meristem. Throughout its benthic life, *T. testudinalis* survives better on the smooth, plane surface of *C. circumscriptum* than elsewhere, and *T. testudinalis* larvae probably are specifically attracted to the alga (Steneck 1982). *C. circumscriptum* usually is not found in the absence of *T. testudinalis*, because this limpet keeps its habitat and food supply free of epiphytes and staves off competitors. The thickened epithallus of the alga and host-specificity of the limpet seem to have evolved specifically, resulting in mutualism. Fossil evidence shows this to have happened relatively recently, in the Holocene (Steneck 1991).

In the case reviewed, there is no evidence of any arms race, but mutualism seems to have evolved as a result of historical happenstance.

3. THE EVOLUTIONARY TRANSIENCE AND FORTUITOUS ORIGINS OF MUTUALISMS

(a) *Limpets and host plants*

Other specific associations between limpets and host plants are geologically recent, probably having originated less than three million years ago (Estes & Steinberg 1988). They occur sporadically among taxa (Muñoz & Santelices 1989), suggesting that specific associations and mutualisms are evolutionary fleeting couplings that arise suddenly, only to disappear later when one or both partners become extinct. *Lottia alveus*, for example, suffered widespread extinction in the western North Atlantic when its host, the seagrass *Zostera marina*, was almost wiped out by a pathogen in the 1930s (Lindberg 1990; Steneck 1991).

(b) *Epiphytic cleaners*

Epiphytes, particularly encrusting invertebrates such as sponges, bryozoans and compound ascidians, sometimes occupy large areas of frondal surface (Seed & O'Connor 1981). This may interfere with photosynthesis (Oswald *et al.* 1984), decrease buoyancy (Wing & Clendenning 1971), and decrease flexibility (Dixon *et al.* 1981) or increase drag (Menge 1975), the last two increasing the risk of tearing or dislodgement. Epiphytic algae can have similar effects and when growing on encrusting forms, they may smother the host to death (Sousa 1979; Steneck 1982). By removing epiphytes, grazers improve the prospects of the host alga (Williams & Seed 1991). For example, *Rhodomela larix* survives, grows and reproduces better when its load of epiphytes is lessened by the grazing activities of amphipods and littorinid snails (D'Antonio 1985).

The change from an association that is only exploitative to one that is mutualistic, may involve but a modest evolutionary step. *Littorina obtusata* and *L. mariae* are sibling species, often occupying the same shores of the eastern North Atlantic, but always ecologically separated by exploiting different algae. *L. obtusata* exclusively uses the long-lived fucoid *Ascophyllum nodosum*. Juveniles feed on sporelings or other delicate epiphytes, but older, larger snails with a strong radular apparatus, graze the host's thallus (Norton & Manley 1990). Commensurate with the longevity of its host, *L. obtusata* is perennial. *L. mariae* on the other hand is an annual, growing only to a relatively small size, it is incapable of grazing the thalli of leathery macroalgae and retains a diet of small, delicate epiphytes and sporelings throughout its life. *L. mariae* lives on kelp laminae and particularly the fronds of *Fucus serratus*. Both substrata are ephemeral or annual, to which the short life cycle of *L. mariae* is suited. The dietary restriction to epiphytes, imposed by small body size, benefits *F. serratus*, however. Fronds grazed by *L. mariae* bear smaller epiphytic loads and consequently are less likely to be torn away by water movement (Williams 1990; Williams & Seed 1991). The mutualism between *L. mariae* and *F. serratus*, therefore, is simply the indirect result of interspecific competition between *L. mariae* and its sibling species, *L.*

obtusata, which has caused the evolution of niche separation through habitat choice and appropriate adjustment of life history.

(c) *Gardening*

Certain tropical-reef fishes, especially pomacentrids (Brawley & Adey 1977; Williams 1980) and temperate-zone limpets (Branch 1981) defend feeding territories, creating scope for controlled levels of grazing and the maximization of sustainable yield. Such 'gardening' is associated with a general scarcity of algal biomass and intense competition among grazers (Branch *et al.* 1991). Occupants rely entirely on their gardens for a supply of food. Consequently, gardening is limited to environments that do not interrupt primary production. For example, gardening limpets on the South African coast are restricted to low-shore levels, where algal production escapes seasonal limitation, and are more frequent on the relatively nutrient-poor east coast than on the enriched, upwelling region along the west coast. Similarly, gardening fishes predominate in the seasonally stable, but nutrient-depleted waters of tropical reefs, where there is intense herbivory (Vine 1974; Hatcher 1988).

Gardens are more productive than surrounding areas (Branch *et al.* 1991), partly because opportunistic, fast-growing algae are encouraged and partly because the algae are maintained in a rapid-growth phase by continual, but not excessive grazing. Horticultural-like practices are sometimes involved. Pomacentrids kill areas of coral, preparing suitable substratum for the settlement and germination of algal spores (Kaufman 1977; Wellington 1982) and some weed the garden by selectively tearing out inedible species (Lassuy 1980). Outside pomacentrid territories, the substratum is dominated by encrusting corallines and repellent foliose algae, whereas within the gardens grow delicate, filamentous forms such as *Polysiphonia* (Sammarco 1983). Unlike most other herbivorous reef fishes, pomacentrids are unable to triturate and digest physically or chemically defended algae, but with their closely spaced, needle-like teeth they are able to efficiently graze fine, filamentous forms. The garden therefore provides the fish with a continual supply of food and the algal crop with protection from overgrazing by other herbivores.

In contrast to pomacentrids, limpets increase above background the level of grazing within their territories (Branch *et al.* 1991). This relatively intense grazing, however, is not indiscriminate. *Patella longicosta* and *P. cochlear* crop the algae in such a way as to leave a reticulated pattern of ridges. This maximizes the surface area of plant growth and hence productivity (Branch 1981). The intense grazing favours fast growing, but competitively inferior species, *Ralfsia verrucosa* in the case of *P. longicosta*, *Herposiphonia heringii* and *Gelidium micropterum* in the case of *P. cochlear*. Outside territories, these algae are largely replaced by competitively dominant, encrusting forms, indeed *G. micropterum* has only been found within *P. cochlear* gardens (Branch 1975). Again, the garden is of mutual benefit to gardener and crop plant, the former gaining

an assured supply of food, the latter a refuge from competitors.

Gardening results from contest competition for food and may disappear, even within a species, where competition is less intense. *Patella barbara* and *P. miniata* garden on the relatively impoverished east coast of South Africa, but graze non-territorially on the enriched west coast (Branch *et al.* 1991). The 'crop' plants of most gardening herbivores are simply widespread, opportunistic algae that are able to support persistent grazing and find competitive refuge within gardens. In some cases, there is evidence of 'fine tuning', for example the optimal cropping behaviour of certain limpets and perhaps the confinement of *Gelidium micropterum* to *Patella cochlear* territories (above), but gardening remains basically an indirect consequence of contest competition.

4. DISCUSSION

It is clear from the data reviewed above that a significant proportion of aquatic plant–animal interactions occur between species with relatively similar generation times, in contrast to the situation pertaining in the terrestrial analogues. However, it is not at all clear that such interactions can be usefully viewed as coevolutionary events.

Adopting a selfish-gene viewpoint, the strongest candidates for coevolution would be the different loci in the nuclear genome. Such loci are strongly constrained by the process of cell division to replicate at the same rate, although molecular mechanisms exist which permit some differences in rate of replication among loci (see Dover (1988) for examples). In these tightly constrained systems, there is clearly a short-term evolutionary advantage for mutually beneficial alleles at different loci to become tightly linked to form 'coadapted gene complexes'. One might expect that the outcome of such selection would be the production of a genome consisting of one tightly linked gene complex (but see Turner 1967). At one level, this has been achieved in the sense that the genomes of extant species comprise loci that cooperate with one another. The persistence of recombination among loci, however, is clear evidence that there is some disadvantage associated with too close an association. If loci become too tightly linked (over connected) there would be a loss of evolutionary flexibility in the system with the concomitant danger of an increased probability of extinction, clearly shown for example by obligate clonal organisms (Hughes, 1989).

To maintain a stable, coevolved partnership between interacting species whose life cycles are not as closely constrained as genes within a genome, much stronger 'genetic feedback' is required. That is, the connectedness of such systems must be high. This, however, is a precarious situation, because it increases the sensitivity of the system to environmental change (see the example of *Lottia alveus* and *Zostera marina* reviewed above).

Of course it is possible for mutualisms to stabilize and assume paramount importance at higher taxonomic levels (Boucher *et al.* 1984). Quintessential

examples include the consortia of microbially derived organelles of eukaryotic cells (Margulis 1981) and the endosymbiosis between dinoflagellates and corals (Spencer Davies 1991; Smith, this symposium). Such evolutionarily stable endosymbioses originally involved at least one unicellular partner, which could complete its life history within the confines of the association. Stability becomes more tenuous when one partner cannot live entirely in association with the other. The ascoglossan–chlorophyte association, falling short of mutualism, probably represents the evolutionary limit to an endosymbiotic relationship between a herbivore and its multicellular food plant.

For coevolution, in the sense of reciprocal, stepwise evolution to occur, the balance between the benefit of the interaction in the short term and the greater fragility of the system in the longer term, due to increased connectedness, must be biased strongly in favour of the benefit. With the exception of some of the endosymbiotic mutualisms described above, the strength of genetic feedback needed to maintain the mutualism may result in the costs outweighing the benefits, with the result that the majority of existing species interactions fall short of coevolved mutualisms.

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Discussion

N. KNOWLTON (*Smithsonian Tropical Research Institute, Balboa, Republic of Panama*). One of the biggest differences between marine and terrestrial ecosystems seems to be the relative lack of specialist herbivores in the sea. What are Professor Hughes' explanations for this apparent pattern?

R. N. HUGHES. We favour the idea (Hay & Fenical 1988) that insects are able, with consistent accuracy, to locate specific host plants, whereas drifting propagules of aquatic invertebrates are not. Certain insects, notably aphids (J. H. Lawton, personal communication), also are liable to uncontrolled drift, but aphids reproduce profusely by apomictic parthenogenesis, vastly increasing the chance of the clonal genome reaching suitable host plants (Hughes 1989). This interpretation, however, should be viewed cautiously. Marine propagules are often able to postpone settlement if suitable substrata are not located. They are, moreover, strongly attracted to substratum-specific stimuli.

S. B. MALCOLM (*Department of Biology, Imperial College, Silwood Park, U.K.*). Are differences in scale between marine and freshwater ecosystems likely to influence plant–herbivore interactions? For example, are water-soluble, plant chemical defences against aquatic herbivores more likely in small, freshwater ponds with fairly simple physical characteristics than in large volumes of seawater? Could differences in light penetration between marine and freshwater systems mean that metabolic pathways for the synthesis of antiherbivore chemical defences are constrained in different ways? Thus should we expect different kinds of defences in various aquatic systems that also differ from those of terrestrial systems?

R. N. HUGHES. Size of the water body apparently does not constrain the effectiveness of water-soluble, chemical defences. In freshwater ponds, cyanobacteria produce endotoxins that are retained within the cell, whereas in the open sea dinoflagellates leak exotoxins into the water. Oceanic water masses retain their identity for some considerable time and local concentrations of dinoflagellate toxin can be sufficient to impair somatic and population growth of herbivorous copepods (Huntley *et al.* 1987).

Chemical defences of benthic macroalgae most obviously differ from those of higher plants in the lack of alkaloids, halogenation and the derivation of polyphenolics from phloroglucinol. Lack of alkaloids probably can be explained by nitrogen limitation, seawater generally being depauperate in this nutrient (Hay & Fenical 1988). Plant-like bryozoans, on the other hand, produce alkaloids (Carle & Christophersen 1980), but they have a nitrogen-rich diet. Halogenation is enigmatic; it occurs in bryozoans (Carle & Christophersen 1980) and perhaps may be concerned with antifouling properties. The central role of phloroglucinol in macroalgae may be a phylogenetic legacy. Because macroalgae are largely of intertidal or shallow subtidal habit, it is perhaps unlikely that light penetration would constrain the kinds of metabolic pathway involved in the production of secondary metabolites. The above ideas, however, are speculative and more data are needed to answer these interesting questions.

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P. J. GRUBB (*Botany School, University of Cambridge, U.K.*). Among land plants the ones with most notable defences against animals include both species that grow particularly slowly, e.g. semi-desert cacti, and species which grow particularly fast, e.g. spiny or poisonous gap-demanders in forest such as brambles and deadly nightshade. Professor Hughes' account suggests that among seaweeds chemical defences are well developed in the slowest-growing species but poorly developed or absent in the fast-growing 'gap-demanders'. Could he please comment on this difference?

R. N. HUGHES. Growth rate and repellency are not strongly correlated among seaweeds. Phlorotannins are present not only in modestly growing fucoids, but also in rapidly growing kelps such as *Macrocystis pyrifera* (North 1971). Species of *Laurencia*, comparable in growth, may be strongly defended or lack defences altogether. Here, defensiveness is correlated with the risk of herbivory (Hay & Fenical 1988).

Defences are conspicuously absent among green seaweeds. Apart from certain strongly defended, perennial occupants of tropical reefs, chlorophytes are characteristically flimsy, opportunistic plants. They are temporary gap-fillers, of poor competitive ability and attractive to herbivores (Littler & Littler 1980). They grow fast and easily regenerate from fragments that accidentally escape digestion and become voided in the faeces of herbivores (Santelices & Ugarte 1987). Undefended chlorophytes, then, are equivalent to ephemeral or annual herbs. Defended, perennial gap-fillers, equivalent for example to brambles in forests, include certain kelps such as *Agarum cribrosum* (Dayton 1975). The situation probably is not fundamentally different between terrestrial and marine vegetation.

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