

STRATEGIES AGAINST
GENERALIST HERBIVORES
IN MARINE MACROALGAE

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1.0 INTRODUCTION

Marine macroalgae, or seaweeds, are visible by unaided eye in the marine environment. They can be found growing mainly in the inter-tidal and shallow sub-tidal zones. Both physical and biological factors influence the distribution and abundance of seaweeds. Herbivory and competition influence the growth rate and reproductive output of algae (Berner,1990). Herbivory has been shown to play a role in determining diversity, abundance, and species composition of seaweeds in shallow water benthic communities (Hay et al,1988c; van Alstyne,1989).

Generalist herbivores consume a wide variety of food plants, often with a ranked order of acceptance or preference (Lubchenco & Gaines,1981). These herbivores are generally larger in size, allowing them to be highly mobile. In marine communities most fish, sea urchins, and many gastropods are generalist herbivores. Specialist herbivores by contrast feed on a few plant species or certain tissues, like fruits or seeds. Specialist herbivores of marine macroalgae are rare (Hay & Fenical,1988; Hay et al,1989).

The definition of strategy (Macquarie Dictionary 1989) implies awareness and premeditation. In this essay it is used to mean traits, both physical and chemical, that have evolved to increase the survivorship of an individual. In marine macroalgae strategies against herbivores have evolved in response to the high concentration of herbivores that are present in the shallow sub-tidal zone. It is not surprising then that on coral reefs, where the greatest concentration of generalist herbivores occurs (Hay & Fenical,1988), most seaweeds exhibit some type of strategy. Strategies against herbivores can be divided into escapes and defenses. Escape strategies reduce the probability of the seaweed being found by a herbivore (Lubchenco & Gaines,1981). Examples of escapes are avoidance of herbivores in space and time, growing in association with unpalatable species, and rapid growth that exceeds the rate of grazing. Defense strategies operate by lowering the relative preference of a seaweed as perceived by a herbivore (Lubchenco & Gaines,1981). Defenses can be either morphological or chemical. In areas of intense herbivory many seaweeds manifest both.

In this essay I will discuss the different strategies introduced above. Examples from the literature will be presented for each of the strategies. The important questions that arise from these patterns are: Why are there so many types of strategies?; How did strategies against herbivores evolve? The question of the evolution of strategies involves that of multiple benefits. These issues will be dealt with later in this essay.

2.0 STRATEGIES AGAINST HERBIVORES IN MARINE MACROALGAE

Herbivores have a major influence on macroalgae in both temperate and tropical shallow water communities (Lubchenco & Gaines, 1981). On coral reefs it is estimated that 60-97% of the primary production is consumed by herbivores (Hay & Fenical, 1988). Macroalgae are somehow able to survive and reproduce under these seemingly adverse conditions. To maximize individual fitness in the presence of herbivores, requires strategies that reduce the probability of damage resulting from grazing.

Many different classifications of strategies against herbivores have been suggested in marine macroalgae (Hay & Fenical, 1988; Hay, 1991; Littler et al., 1983; Lubchenco & Gaines, 1981; Norris & Fenical, 1982; Steneck, 1988). Lubchenco & Gaines (1981) have presented a definition which lends itself to developing a concise and unambiguous classification of strategies against herbivores. Lubchenco & Gaines (1981) define expected herbivore damage to an individual seaweed, in a given space, at a given time as:

$$P(En) P(Ea_{En}) E(1-w \text{ given } En \ \& \ Ea)$$

where, $P(En)$ is the probability of being encountered, $P(Ea_{En})$ is the probability of tissue consumption once encountered, and $E(1-w \text{ given } En \ \& \ Ea)$ is the reduction in fitness after herbivore attack relative to an undamaged plant. From this definition it is evident that there are two classes of strategies against herbivores. Firstly an escape component, $P(En)$, where there is no contact between herbivore and seaweed. This is termed non-coexistence escape by Lubchenco and Gaines (1981). Secondly a defense component, $P(En_{Ea})$, where the seaweed is encountered but not, or only partially consumed. This is "either because it (the seaweed) is inedible (i.e. it has some structural or chemical defense that confers a co-existence escape) or because there are more preferable plants available." (Lubchenco & Gaines, 1981).

Escapes are the primary strategy against herbivores. These are influenced by, (1) the size, longevity, and chemical composition of the seaweed; (2) the sensory acuity, mobility (a function of size), and density of herbivores; and (3) physical and biotic factors of the environment that can influence the strength and range of the stimulus, as well as the duration of the encounter. Escapes can occur in time. Seaweeds can become prolific during seasons when herbivores are less abundant (Lubchenco & Cubitt, 1980; Hay, 1986). Escapes can also be of a spatial nature. Seaweeds can grow in habitats where herbivores are less likely to be encountered (Lubchenco & Gaines, 1981; Gaines & Lubchenco, 1982), or grow in association with plants or animals that are avoided (Hay, 1986; Littler et al, 1986; Littler et al, 1987). Rapid growth and escapes in size are the third type of escapes. These can be manifested either as small algae growing in a cryptic fashion,

or as rapid growth to a large size where the seaweed is less susceptible to herbivory (Den ton et al.,1990; Hay,1981).

Defenses are the secondary strategy in the macroalgae. They are effective when the seaweed is encountered by a herbivore. Defenses influence the probability that a herbivore will consume part of an encountered seaweed. Defense strategies found in seaweeds are: (1) morphological attributes like size, shape, and toughness (Litter & Littler,1980; Littler et al.,1983; Paul & Hay,1986; Steneck,19 88); (2) the presence of secondary metabolites or chemical defenses in the form of feeding deterrents and digestibility reducers (Norris & Fenical,1982; Hay & Fenical,1988); and (3) nutritional parameters of the seaweeds. Chemical defenses are the best understood defenses as they have been the subject of intense research in both terrestrial and marine habitats.

2.1 TEMPORAL ESCAPES

This strategy reduces a seaweed's susceptibility to herbivory because herbivores are not active or present all the time. Temporal escapes can occur when there is a predictable change in herbivory over a certain period of time. This can include diel variations in herbivore assemblages (diel escapes) and seasonal changes in the composition of the herbivore community (seasonal escapes).

1) Diel escapes:

The pan-tropical genus *Halimeda* experiences a reduction in grazing of susceptible, young, developing tissues when producing new segments at night, because herbivory from reef fish is low at this time (Hay et al,1988d). Plant portions more than 48 hours old are low in food value and well defended morphologically, therefore relatively resistant to herbivory. Young, newly produced segments have a higher nutritional value, but are only moderately more susceptible to herbivores as they contain high concentrations of terpenoid feeding deterrents. These concentrations drop as the segment ages and becomes increasingly calcified.

2) Seasonal escapes:

Heteromorphic seaweeds exhibit two or more morphologies, often representing different stages of their life cycle. Lubchenco and Cubit (1980) found several species of seaweeds on temperate east Atlantic shores exhibit such heteromorphic life cycles. During the summer when herbivory is high these macroalgae grow as crustose morphologies, while during the winter months when there is little grazing, they occur as upright morphologies. Caging experiments showed that the upright morphology could survive in summer if the major herbivore, *Littorina littorea*, was excluded. *Littorina* preferred the upright morphologies over the crustose forms in laboratory experiments.

The establishment of crustose forms may require the removal of competing upright morphologies by herbivores (Clayton,1990).

Macroalgae that are not heteromorphic should occur in habitats with predictable herbivory, either as crustose or upright forms depending on the intensity of grazing. Fluctuating herbivory, on a predictable basis (seasonal), should result in alternating heteromorphic generations under the influence of natural selection. With unpredictable herbivory both morphologies should be found, with the dominant morphology varying with grazing pressures (Hay,1991; see Lewis et al,1987).

2.2 SPATIAL ESCAPES

Seaweeds occupy habitats where herbivores rarely feed. These are refuges in space. Hay (1991) differentiates between three categories, among-, within-, and micro-habitat refuges. However the first two categories are very similar and overlap in some cases. The among habitat refuges cited by Hay (1991) are deeper fore reefs, shallow reef flats, and sandy lagoons. These same habitats are again used as examples of within habitat refuges. I have therefore amalgamated Hay's (1991) first two categories into one, namely among and within habitat refuges are now between habitat refuges. This is more consistent with the terminology employed by Hay in an earlier paper (Hay,1984) and Lubchenco & Gaines (1981;1982). In this essay I therefore distinguish between macro-habitat refuges and micro-habitat refuges.

1) Macro- or Between Habitat Refuges:

Differences in herbivory exist between habitats. On a biogeographic scale this is evident as latitudinal gradients of diversity, biomass, and morphology of both macroalgae and herbivores (Gaines & Lubchenco,1982). There is a general increase in species richness of both seaweeds and herbivores towards the tropics. The average size of the macroalgae decreases. Concomitantly that of the herbivores increases because of the larger number of herbivorous fish on coral reefs. Therefore, random spatial and temporal escapes become less common from temperate latitudes towards the tropics.

On a smaller scale, such as a coral reef, macro-habitat refuges will determine where herbivore susceptible seaweeds will occur. Species of macroalgae that are not normally found on the slope because of fish grazing often persist on reef flats where shallow water (Lubchenco & Gaines,1981) or low habitat heterogeneity (Hay,1984; Hay,1991) limits grazing by fish.

2) Micro- or Within Habitat refuges:

Refuges in habitats that are otherwise relatively uniform result in spatial mosaics. On coral reefs patchiness is generated by territorial pomacentrids (damselfishes) that selectively "weed out" certain species of macroalgae which are unpalatable (Hay,1991). Thus, in these defended pomacentrid territories, there is an increase in abundance and biomass of palatable macroalgae, compared to the rest of the reef slope.

Micro-habitat heterogeneity may influence herbivore foraging efficiency and seaweed productivity (Lubchenco & Gaines,1981). On New England rocky shores *Littorina littorea* forages less effectively in cracks than on homogeneous surfaces. Therefore, *Fucus* sp. sporelings tend to establish better in cracks (Lubchenco & Gaines,1981).

2.2.1 Associational Escapes:

These are a special subset of within habitat escapes that have only recently been discovered. Growing in association with unpalatable seaweeds or sessile animals allows certain palatable macroalgae to benefit from reduced herbivory (Littler et al,1986; Littler et al,1987). These associations result in an increase in the local species diversity of seaweeds, even where high grazing pressures and competitively dominant macroalgae are present. In associations palatable seaweeds often exhibit reduced growth, but this cost to fitness is much less than the normally experienced cost of grazing.

Styopodium zonale is a herbivore resistant brown macroalgae which contains chemical compounds that have been found to be toxic to fish, even at low concentrations (Hay et al,1987b). A doubling in species diversity of palatable seaweeds around *Styopodium* was found by Littler et al (1986). These macroalgae enjoyed greater survivorship when associated with *Styopodium*. Fish recognize *Styopodium* both visually and chemically. Littler et al (1987) found seaweeds also showed increased survivorship when associated with *Gorgonia ventalina* (sea fan) or *Millepora alcicornis* (fire coral). Hay (1986) found similar associations occurring around macroalgae of the genera *Dictyota* and *Halimeda*.

Seaweeds can be cryptic by growing in locations avoided by or inaccessible to herbivores. Epiphytes growing on less preferred macroalgae can escape from herbivores in this way. In summer, when most herbivorous fish are present, the temperate palatable macroalgae *Hypnea* sp. grows on the less preferred *Sargassum* sp. and *Padina* sp. (Hay,1986). In winter when there are few fish *Hypnea* no longer occur as epiphytes, but as macrophytes. These compete for space with the less preferred species. As an epiphyte *Hypnea* has a lower growth rate (only 14-19%) than when it occurs as a macrophyte. This is still advantageous to the algae as the macrophyte form is more susceptible to grazing. Epiphytism may be a strategy to compete for space that is already

occupied by other species. This will increase the local diversity. Epiphytism can also act as a herbivore evasion strategy for highly preferred species of algae.

2.3 RAPID GROWTH AND SIZE ESCAPES

These strategies are difficult to classify as they could be either escapes or defenses. The effectiveness of size escapes depends on the herbivore involved. A large seaweed on the coral reef may be able to escape grazing by invertebrates but not fish. However this is confounded by the presence of possible morphological and chemical defenses in these macroalgae. Conversely large temperate kelps may escape from fish grazing, but not from smaller gastropods that can move about on the seaweed and feed.

In the temperate fucoids size-related escapes from herbivory may be species specific (Denton et al,1990). Herbivore resistance in *Fucus vesiculosus* is restricted to individuals of more than three centimeters in length. Small individuals must pass through a grazing bottleneck where they are rapidly eliminated by *Littorina littorea*. However, the abundance of small *Fucus spiralis* is not affected by grazing, while the larger plants are affected by herbivores at natural densities. Denton et al (1990) found that small *F. vesiculosus* were not defended chemically by polyphenols while *F. spiralis* were. Rapid growth would be an important strategy in small *F. vesiculosus*.

On coral reefs there is a low standing crop of seaweeds but a rapid turnover from grazing (Berner,1990). Seaweeds are generally small except when defended or growing in escapes. Rapid growth is therefore selected for in this intensely grazed habitat. Turf algae are a specialized morphological growth form of some species of tropical seaweeds (Littler & Littler,1980). Grazing is advantageous to the turf algae as it reduces self-shading and localized nutrient depletions caused by the tight growth form. Growth occurs in the upper regions, more susceptible to herbivores, where photosynthetic tissues are concentrated. As a consequence there is rapid growth to replace tissues continually lost to herbivores, resulting in a rapid turnover rate (Hay,1981). It may be argued that rapid growth is not a true escape but rather allows the algae to tolerate grazing.

2.4 MORPHOLOGICAL DEFENSES

Defenses differ from escapes. Defenses are important in deterring herbivores from consuming the seaweed once it has been encountered. Morphological defenses are structural features of macroalgae that reduce their susceptibility to herbivory. The two main types of morphological defenses are growth form and toughness.

1) Growth Form:

The growth form of a seaweed is an important factor that influences which herbivores it is susceptible to and in which habitats the seaweed can survive. For example the brown macroalga, *Lobophora variegata*, exhibit three distinct growth forms (ruffled, decumbent, and encrusting), depending on environmental characteristics including light, depth, exposure, and herbivore abundance (Coen & Tanner, 1989). The ruffled form is highly palatable to fish and crabs. It is restricted to areas of low herbivore abundance. The decumbent form is highly unpalatable (comparable in feeding bioassays with *Styopodium zonale*), even though it has the highest calorific value and organic content of the three forms. It is found in areas of moderate herbivory, but excluded from areas with high grazing pressures, except in spatial refuges. The low preference of this form may be due to chemical compounds present in the thallus (Coen & Tanner, 1989). The encrusting morphology is present in areas of intense herbivory. It is inaccessible to most grazers because of its tightly adherent growth form.

Herbivory is a major factor influencing thallus form in *L. variegata*. Morphological and chemical traits are likely to account for the differences in susceptibility to herbivory. The three morphologies are possibly genetically distinct ecotypes that have diverged in response to locally different physical and/or biological environmental influences. Plasticity of growth form may be an important strategy for tropical macroalgae to cope with locally intense but patchy herbivory.

Morphological variation is exhibited in many marine macroalgae associated with different coral reef habitats (Lewis et al, 1987). *Padina jamaicensis* exhibits two different morphologies depending on the intensity of fish grazing. After experimentally reducing grazing using cages, the herbivore resistant, prostrate, turf form of *P. jamaicensis* "switched" to the more susceptible, foliose morphology within 96 hours. This phenotypic response to grazing may represent an important adaptive strategy. It allows seaweeds exhibiting morphological plasticity to persist in intensely grazed marine habitats, through the ability to respond rapidly to spatial or temporal fluctuations in herbivory.

Turf algae are a specialized morphological growth form of some species of tropical seaweeds. By growing as tight clumps turf forms are more resistant to both desiccation and herbivory (Littler & Littler, 1980). This allows turf algae to grow in environments where herbivory is high, wave action is strong, and there are lengthy periods of emersion. Turf algae, although highly visible, may be inaccessible to most herbivores. The tightly compact, low profile growth form of these algae makes it difficult for grazing fish to get a good mouthful. Also urchins are only observed to graze along the edges of the turf, as they cannot get a firm grip upon the algae and are susceptible to being swept off by wave action (Hay, 1981). Grazing is advantageous to the turf algae as it reduces self-shading and localized nutrient depletions that are caused by the tight growth form.

Growth occurs in the upper regions, more susceptible to herbivores, where photosynthetic tissues are concentrated. This results in rapid growth to replace tissues continually lost to herbivores, resulting in a high turnover rate. Turf algae are morphologically plastic and tend to more arborescent forms when grazing is reduced.

2) Toughness:

Calcification and structural carbohydrates are often cited as morphological defenses (Paul & Hay,1986; Padilla,1989; Steneck,1988; Watson & Norton,1985). Calcification is probably the most evident morphological defense in tropical seaweeds, while structural polysaccharides are prevalent in temperate kelps.

The functional form model developed by Littler and Littler (1980;1983), and as adapted by Steneck and Watling (1982), quantified toughness by using a mechanical approach. The functional form model attempted to explain morphological trends evident across divisions of macroalgae. Seaweeds were grouped into sheet-like, filamentous, coarsely branched, thick leathery, jointed calcareous and crustose coralline algae (Table 1). The toughness (= resistance to penetration) increased through this series. Toughness correlated negatively with the grazing preferences of urchins (Littler & Littler,1980), gastropods (Steneck & Watling,1982), and fish (Littler et al ,1983). Sheet-like and filamentous algae were heavily grazed, while the calcareous groups were least consumed.

Littler et al (1983) interpret their results to indicate that herbivore preference is a function of the degree of toughness (calcification or structural polysaccharides) and calorific value of the seaweeds. Tougher macroalgae, such as thick leathery and calcareous crustose types, have a correspondingly lower calorific value which decreases their digestibility and energetic return to the herbivore (Hay,1991). The calorific values however are not significantly different among the groups of the non-calcified macroalgae (Littler et al, 1983). It is possible that only the calcium carbonate in the crustose forms makes them less nutritional.

The main problem with the methodology employed by Littler & Littler (1980;1983) is that it does not adequately appraise ecological toughness. This varies with the anatomy of both the mouthparts of the herbivore and the seaweed (Padilla,1985; Padilla,1989; Watson & Norton,1985). Mechanical forces used to determine toughness must therefore simulate those that the herbivore applies to the macroalgae.

TABLE 1: Functional groups of macroalgae based on increasing toughness (Steneck & Watling,1982; Littler et al,1983).

Functional group	External morphology	Internal anatomy	Examples of genera
Filamentous algae	delicately branched with holdfast	lightly corticated	<i>Cladophora</i> , <i>Ectocarpus</i> may include sporelings of other groups
Sheet-like	foliose or thin tube like morphology	only one or two cells thick	<i>Ulva</i> , <i>Dictyota</i>
Coarsely branched	upright, morphologically complex macrophytes	thick walled cortical cells, larger thin-walled medullary cells	<i>Laurencia</i> , <i>Caulerpa</i> , <i>Chnoospora</i>
Leathery macrophytes	thick blades and branches, can grow very large (70 m)	extensively corticated, morphologically differentiated	<i>Sargassum</i> , <i>Fucus</i> , <i>Lobophora</i>
Articulated calcareous	upright, articulated	short calcareous segments connected by flexible intergeniculae	<i>Halimeda</i> , <i>Amphiroa</i> , <i>Corallina</i>
Crustose calcareous	prostrate,	encrusting heavily calcified rows of cells	<i>Porolithon</i> , <i>Lithothamnion</i>

Padilla (1985;1989) used excised radulae of docoglossan limpets to determine the rasping forces that would be applied in normal feeding on macroalgae, with various degrees of calcification. Contrary to previous hypotheses (Steneck & Watling,1982; Litter et al,19 83) less force was required to remove tissue from the calcified macroalgae than from uncalcified seaweeds. The calcified seaweeds are suspected of being more brittle, while the uncalcified macroalgae tend to yield under applied force, requiring greater strength to break. Padilla (1989) concludes that toughness is not increased with calcification and cannot be indicative of herbivore preference . However as pointed out by Padilla (1989): "The degree to which thallus form and calcification influence the susceptibility of macroalgae to docoglossan limpets may not be the same for other herbivores which feed in a different manner or have a different feeding apparatus."

Clearly toughness, as defined in the functional form model of Litter et al (1983), is not applicable to all herbivores. Overall the functional form model is still a good indicator of various

life history strategies evident in the macroalgae. Morphological defenses are difficult to quantify as they tend to vary in effectiveness depending on the herbivore involved.

2.5 CHEMICAL DEFENSES

Compounds used as chemical defenses are secondary metabolites, sometimes termed allelochemicals (Geiselman & McConnell,1981). These are chemicals that are intermediates from the syntheses of primary biochemical pathways. Secondary metabolites used as defenses against herbivores are found in most plants, including seaweeds. More than 1000 chemical compounds with diverse structures and functions have been isolated from mainly tropical macroalgae (Hay & Steinberg,1991). These include terpenes, aromatic compounds, acetogenins, amino-acid derivatives, polyphenols and halogenated compounds (Hay & Fenical,1988). Halogenated compounds are unique to marine macroalgae because of the abundance of the precursors in seawater.

Secondary metabolites function primarily as herbivore deterrents, either by reducing the palatability or nutritional quality of the seaweed, or via toxic effects which reduce the fitness and survivorship of the herbivore (Norris & Fenical,1982; Steneck,1988).

In temperate brown macroalgae the feeding deterrent effects of polyphenols are the main defense against gastropods and sea urchins (Geiselman & McConnell,1981; Steinberg,1988). Experimental work has shown a negative correlation between phenol content and feeding preference of the various parts of kelps (Steinberg,1984; Johnson & Mann,1986). Intraplant variations in three temperate kelps were analyzed by Tugwell and Branch (1989). They found the more herbivore susceptible tissues such as outer meristoderm and reproductive structures contained high concentrations of polyphenols. The induction of increased polyphenol synthesis after simulated herbivore attack (van Alstyne,1988) further corroborates the activity of some polyphenols as herbivore deterrents.

Secondary metabolites are found in the most common and least preferred seaweeds on coral reefs (Hay,1984; Hay et al,1988c; Lewis,1985; Paul et al,1988). Many of the common tropical seaweeds have been chemically analyzed and pharmacological and ecological bioassays performed with the active compounds (Hay et al,1988c; Lewis,1985; Norris & Fenical,1982). The secondary metabolites were found to have a significant role in protecting these macroalgae from fish and other herbivores (Hay et al,1988c). However, not all seaweeds that contained secondary compounds showed a reduced susceptibility to fish. Hay (1984;1986) proposed that chemical defenses are not effective against all herbivores. The herbivore deterrent action of these compounds is often highly specific. Similar compounds, or even the same chemical, can have different effects on different

herbivores (Lewis,1985; Hay,1991). This action is not an intrinsic property of the molecule per se, rather it depends on interactions with the biochemistry of the herbivore involved (Hay et al,1988a;1988b).

The secondary compounds of the brown macroalgae *Dictyota dichotoma* that deter feeding by herbivorous fish do not deter, or may even increase, feeding by small, sedentary herbivores (mesograzers) such as amphipods and polychaetes (Hay et al,1987a;1988b). Hay et al (1987a) postulate that predation by herbivorous fish may be major factors influencing the selection of unpalatable seaweeds as a food source and habitat for mesograzers.

For a chemical defense to be successful against herbivores it must act upon primary metabolic processes (McKey,1979). These very same processes probably also occur in the macroalgae that produce the chemicals, resulting in the problem of autotoxicity. Mechanisms of circumventing autotoxic effects in seaweeds include, (1) the segregation of polyphenols and other chemicals into vacuoles, or specialized structures; (2) the activation of toxic secondary metabolites from precursors when damaged, as in *Halimeda* sp.; and (3) detoxification systems if leakage of the compounds occurs (Hay & Fenical,1988; McKey,1979; Paul & van Alstyne,1988).

If a chemical is highly deterrent to herbivores, it is likely to mean high metabolic costs will be involved in the production, segregation, and possible degradation of the chemical. Highly deterrent chemicals should be allocated to tissues that are more susceptible to grazing. Young, newly produced segments of *Halimeda* sp. are of higher nutritional value, but are only moderately more susceptible to herbivores as they contain high concentrations of terpenoid feeding deterrents (Hay et al,1988d). These concentrations decrease as the segment ages and becomes increasingly calcified.

Chemical variation can also occur between individual plants. In some cases this may be adaptive. Seaweeds from the intensely grazed reef slope often produce more diverse secondary metabolites and in higher concentrations than counterparts in the lagoon or on the reef slope where herbivory is less (Hay,1984; Paul & Fenical,1987).

3.0 COSTS AND BENEFITS OF DEFENSES

Herbivory is assumed to be an intense selective force in the evolution of marine macroalgae and is an important factor in the organization and development of communities of seaweeds. Herbivory is strongly implicated in driving natural selection for defenses and escapes because grazing reduces the growth, reproduction and survival of individuals (Crawley,1983; Littler et al,1986; Rhoades,1979). In tropical coral reef systems herbivory is intense so seaweeds often contain a combination of defenses and/or escapes.

3.1 MULTIPLE DEFENSES

In habitats with a diverse assemblage of herbivores multiple defenses may be necessary for seaweeds to survive. With a higher diversity of herbivores the probability of one circumventing any single defensive trait increases (Hay et al,1988c). In coral reef seaweeds the production of both a calcareous thallus and secondary metabolites is often correlated with low herbivore preference for these algae. Up to 85% of tropical seaweeds studied by Paul & Hay (1986) possessed chemical defenses as well as being calcified. This may be a result of the ineffectiveness of calcification as a defense against certain groups of herbivores (Padilla,1989). Only 39% of the non-calcified macroalgae produced chemical deterrents (Paul & Hay,1986).

The pan-tropical genus *Halimeda* is heavily calcified (50-90%) and also heavily defended by secondary metabolites (Paul,1985). These seaweeds are widely distributed and abundant on coral reefs where grazing by fish is intense. The calcified brown macroalgae *Padina* sp. are also defended by polyphenols in low concentrations but are very susceptible to herbivory (Lewis,1985). However the chemically defended genus *Caulerpa* is not calcified, but is very resistant to fish grazing (Lewis,1985; Paul & Hay,1986). Different species of macroalgae often have different combinations of defenses that vary in their effectiveness.

3.2 DEFENSE THEORIES

Defense theories assume that plants (both terrestrial and aquatic) evolve strategies to reduce the detrimental effects of herbivory. Herbivores should concurrently evolve offensive adaptations to counteract these defenses (Rhoades,1979; Fox,1981; Crawley,1983). Chemical defenses are the most studied as the concentrations, and their effects on herbivores, can be quantified. Other

defenses and escapes are very difficult to quantify, as exemplified by the debate about morphological toughness (Littler et al,1983; Padilla,1989).

Secondary metabolites are proposed to have evolved from the diversion of energy and nutrients from primary biosynthetic pathways (Rhoades,1979). Secondary metabolites as chemical defenses could have originated either by, (1) the altered substrate specificity of enzyme systems catalyzing the biosynthesis of common amino acids; and (2) new defensive compounds being produced by regulatory changes in pre-existing pathways, resulting in the accumulation of an intermediary metabolite not previously used.

The production of chemical defenses against herbivores entails metabolic costs that are assumed to be reflected in a decreased growth rate, reproductive output, or competitive ability (Rhoades,1979; Hay,1984). The cost of defenses is theoretically measured in terms of the diverted nutrients and energy used in the secondary metabolites (Hay et al,1988c) and includes such factors as, (1) the cost to manufacture, translocate, and sequester the secondary metabolites; (2) the cost of maintenance of these compounds as well as the cellular compartments in which they are stored, especially if autotoxic; (3) an estimate of the reduction in competitive ability, compared to non-defended plant genotypes in a herbivore free habitat (Chew & Rodman,1979).

A number of theories revolving around cost-benefit hypotheses have been developed in an attempt to explain the variation evident in chemical defenses. These include the Plant Apparency Model and Optimal Defense Theory, the Resource Availability Hypothesis, and the concept of Induced Defenses.

3.2.1 Plant Apparency And Optimal Defense Theory:

The Plant Apparency Model (Feeny,1976; Rhoades & Cates,1976) has been one of the most influential models of plant-herbivore interactions. This model contrasts two very different types of plants and seeks to explain apparent differences in their defense strategies (Table 2).

The Plant Apparency Model has been attacked from a number of sides in the last decade. Apparency is a factor that varies with each herbivore depending on its sensory acuity, mobility, and the density of the herbivores (Crawley,1983). This is true in the marine environment where fish are very efficient herbivores, especially on coral reefs. The major assumption of the apparency model is that the two types of defense strategies will differ in cost. Quantitative defenses like tannins were assumed to be costly to produce because of their molecular complexity. Swain (1979), Fox (1981) and others have pointed out that once tannins are produced they appear to have minimal maintenance costs, while many of the more active qualitative toxins have high turnover rates. In seaweeds the difference in turnover rates is unclear (see Hay & Fenical,1988).

TABLE 2: The two different types of plants and their defense strategies as proposed by the Plant Apparency Model (Feeny,1976; Rhoades & Cates,1976):

APPARENT PLANTS	UNAPPARENT PLANTS
K-selected: long lived, large, low fecundity	r-selected: short lived, rapid growth, high fecundity
late succession, dominate climax communities	early succession, or rare plants
quantitative defenses	qualitative defenses
dosage dependant action	toxic action at low concentrations
effective against a broad spectrum of herbivores	effective against generalists only, circumvented by specialists
metabolically costly defenses	metabolically cheap defenses
slow turnover rate	high turnover rate
tannins, polyphenols terpenes,	alkaloids, halogens

Tannins were also assumed to have a broad spectrum of action. However, tannins in terrestrial plants may be more specific than initially recognized (Zucker,1983). Tannins and polyphenols decrease the growth and survival of some herbivores qualitatively by feeding inhibition and cell damage, rather than quantitatively by interference with digestion and assimilation, as proposed by Plant Apparency (Hay & Fenical,1988). The effect polyphenols have on feeding varies among marine herbivores and the different types of polyphenols (Steinberg,1988). This suggests that polyphenols are neither uniform in activity nor broadly deterrent as assumed from terrestrial models.

Optimal Defense Theory arises from the assumptions of cost made by the Plant Apparency Model. Optimal Defense Theory (Rhoades,1979) attempts to explain the variation in chemical defenses in terrestrial plants. The theory basically comprises two hypotheses:

- 1) Organisms evolve and allocate defenses in a way that maximizes fitness.
- 2) Defenses are costly in terms of fitness.

If these hypotheses are correct then the following effects should be observable in plants:

- a) Plants will evolve defenses in direct proportion to their risk from herbivores.
- b) Within a plant defenses are allocated in direct proportion to the risk and the value of that tissue in terms of fitness to the plant.

- c) Defenses are costly so that a decrease in commitment to defense should occur when herbivores are absent.
- d) Environmentally stressed plants should be less well defended against herbivores than unstressed plants, as they have fewer resources available for defense.

These corollary hypotheses have all been found to be true in marine macroalgae. Seaweeds in habitats with intense herbivory, such as coral reefs, are often more highly defended. Random spatial and temporal escapes are less common in the tropics than in temperate latitudes, resulting in the need for more effective defenses. Many seaweeds on coral reefs exhibit multiple defense strategies. Refuges will determine where herbivore susceptible macroalgae can occur. Species that are normally not found on the slope because of fish grazing often persist on reef flats where shallow water (Lubchenco & Gaines, 1981) or low habitat heterogeneity (Hay, 1984; 1991) limits grazing by fish.

There are within-plant differences in the allocation of defenses in macroalgae. In the tropical genus *Halimeda* young developing segments are of high nutritional value, but only moderately susceptible to herbivores as they contain high concentrations of terpenoid feeding deterrents (Hay et al, 1988d). These concentrations drop as the segment ages and becomes increasingly calcified. In the temperate kelps high concentrations of polyphenols defend the reproductive structures and meristodermal tissues (Steinberg, 1984; Johnson & Mann, 1986; Tugwell & Branch, 1989). Experimental work has shown a negative correlation between polyphenol content and feeding preference for these defended parts of the kelps (Steinberg, 1984; Johnson & Mann, 1986). Defenses seem to be allocated to more susceptible and valuable tissues.

If defenses are costly then these should be selected against in habitats where there are no herbivores. Where herbivory is predictable defenses should occur only during periods of grazing. Temporal and spatial escapes lend support to this argument. Induced defenses are activated after herbivore attack. They reduce the cost of defense, as they are only produced when needed. Induced defenses are discussed in detail below (section 3.2.2).

When fewer resources are available to a plant then the cost of herbivore damage is likely to be higher than in a non-stressed plant. The Resource Availability Hypothesis of Coley et al. (1985) predicts that resource limited plants will exhibit slower growth and more effective defenses than non-nutrient limited plants (section 3.2.3).

3.2.2 Induced Defenses:

Induced defenses are responses by the plant to herbivore damage, which decrease the negative fitness consequences of further attacks on the plant (Karban & Myers, 1989). Induced defenses include changes in secondary metabolites, morphology, and physiology. The responses to damage may be classified as either active or passive and can be either short or long term, i.e. either act

while the herbivore is still feeding, or deter subsequent attacks. An active response is short term and involves enzymatic activation or de novo synthesis of chemicals (Levin,1971). A passive response will be more long term after tissue removal, especially in nutrient stressed plants. The speed of the response and the concentration of the secondary compounds are important in determining the resistance conferred. Induced defenses may be limited to the directly affected parts, or be effective through-out the whole plant.

The kelp *Fucus distichus* is induced to increase production of defensive polyphenols after herbivore damage (van Alstyne,1988). This response makes the macroalgae less susceptible to future herbivore attacks by affecting its palatability. Foraging by the dominant littorinids was reduced by 50% after the induction of defensive compounds. Just after clipping a preference for these plants was shown by the littorinids, but when the polyphenol levels increased by 20% over two weeks the relative preference for these macroalgae decreased (van Alstyne,1988). Furthermore it was observed that the mechanically damaged macroalgae produced adventitious branches. These are a low preference food item of the littorinids due to the high polyphenol levels (van Alstyne,1988;1989).

Induced defenses may have evolved, (1) as a response to the packaging problems and costs posed by potentially autotoxic chemical; (2) to present a changing target to herbivores and retard counter-adaptation to defenses; and (3) to reduce the cost of defenses by being activated only when necessary (Karban & Myers,1989). Karban and Myers (1989) found that as the density of terrestrial plants increased there was a decrease in the induction of resistance due to the competition for resources.

3.2.3 Resource Availability Hypothesis:

Resources in the form of light, water, and nutrients are important factors influencing plant growth rates. The Resource Availability Hypothesis proposes that as resources become increasingly scarce, the level of investment in defense should increase to an optimum (Coley et al.,1985). If there are few resources, then generally the plant will be slow growing and longer lived than a non-nutrient limited plant. This means any loss of tissues from grazing will be more costly to the resource limited plant. If this is so then one should expect these plants to be well defended. In resource rich environments plants can afford higher losses from grazing, either because rapid growth replaces these tissues, or because defenses are less costly to the plant in terms of resources. Coley et al. (1985;1986) contrast two types of plants growing in environments with different amounts of resources (Table 3).

Nutrient availability was found to play an important role in the production of polyphenols in temperate *Fucus vesiculosus* (Ilvessalo & Tuomi,1989). Polyphenol synthesis was increased under conditions of nitrogen deficiency. As nitrogen is required for protein synthesis these

seaweeds exhibited poor growth. Karban et al. (1989) found that with increasing density or crowding, plants produced fewer and/or less effective defenses. Space is often a valuable resource for plants. More nutrient resources will be available to plants in uncrowded populations, so any response to damage will be more effective. With increased crowding the plants were less able to respond to herbivory and the quality of the damaged plant decreased. Damage resulted in less viable seedlings in crowded plants. This makes these a poorer nutritional source than undamaged plants. However crowding may actually provide more protection as individuals are less apparent. This reduces the probability of grazing on any one individual and may select for a decrease in the defense commitment (C. Johnson pers. comm.).

TABLE 3: Predictions of the types of defenses produced by plants with different resources (Coley et al.,1985;1986).

Resource-poor environment	Resource-rich environment
slow growth	fast growth
long lived	short lived
Immobile (quantitative) defenses	Mobile (qualitative) defenses
metabolically expensive	metabolically cheap
low turnover rates	quick turnover rates
constitutive in tissues	can be induced
carbon based, tannins, polyphenols	toxic, terpenes, amino acid derivatives

The concept of costs and benefits of defenses is by now widely accepted. This is the underlying assumption of the defense theories presented here. The Plant Apparency Model has some difficulties and is not applicable in many cases. This is because of the incorrect assumptions regarding the action of quantitative defenses. It also does not take into account herbivore population dynamics (Fox, 1981). The Plant Apparency Model is too rigorous in its distinctions of the types of plants and can not adequately take into account the variation present in plant defenses. Optimal Defense Theory has been found to be applicable by the validation of the corollary hypotheses, both in terrestrial plants and marine macroalgae. Defenses do seem to be costly to plants. The question remains whether escapes are costly also. Intuitively this is likely to be the case, but difficulties in quantifying the costs may delay confirmation of this. The Resource Availability hypothesis suffers from assumptions made in the Plant Apparency Model, from which it draws heavily. However as resource availability is a continuous variable this hypothesis is more

practical than Plant Apparency. The general concept of resource availability does apply to plant defenses. The Resource Availability hypothesis may be difficult to test quantitatively as many factors influence the production of defenses. More research on macroalgae needs to be undertaken before conclusive statements can be made.

4.0 THE EVOLUTION OF STRATEGIES AGAINST HERBIVORES

From the preceding sections (2.0 and 3.0) it is evident that marine macroalgae possess many different strategies which reduce the detrimental effects of grazing by generalist herbivores. Why are there so many types of strategies against generalist herbivores? How did they evolve? Many strategies against herbivores probably evolved from pre-existing adaptations allowing the plant to cope with its environment.

4.1 Multiple Benefits Of Defenses And Escapes

Strategies against herbivores in marine macroalgae may perform other functions (Hay & Fenical,1988). Rapid growth or large size are common life history strategies in competitively dominant macroalgae. Laminarian and furoid kelps are important canopy forming dominants in temperate benthic communities throughout the world (Clayton,1990). These seaweeds are relatively fast growing and attain a large size enabling them to out-compete other macroalgae.

Mechanical toughness from calcification or structural carbohydrates is prevalent in seaweeds growing in habitats with lots of water motion. The highly calcified crustose red algae are prolific in the high wave energy environments of reef crests (Berner,1990), because wave actions preclude upright fleshy macroalgae. Laminarian kelps dominate in subtidal surge zones because the thallus is very elastic, the holdfast attaches the seaweed securely, and the fronds offer very little resistance to water flow, and are often coated with mucilaginous compounds (Norton et al,1982).

Multiple or alternate functions proposed for secondary metabolites include, (1) protection against UV radiation by polyphenols; (2) allelochemical interactions against other species in the competition for space; (3) inhibition of the settlement of fouling organisms, like spores and larvae; and (4) antibiotic actions against bacteria (Rhoades,1979; Paul & Fenical,1987). With this multitude of other possible functions it is probable that defenses and escapes were not originally strategies against herbivores. Rather these anti-herbivore strategies may have evolved from existing strategies in the seaweed that allowed it to cope with it's environment. This evolution is the result of selection acting upon processes in both the seaweeds and the herbivores.

4.2 Evolution And Co-Evolution:

For evolution to act on defense strategies sufficient variability and heritability must exist. Many chemical defenses have evolved from secondary metabolites involved in other functions. Evolution would result in defense or escape strategies that reduce the cost of herbivory on plant fitness. If plants are defended, herbivores must either adapt to utilizing another food source or co-evolve with the plant to continue utilizing it even though it is defended. Multiple defenses make it harder for herbivores to co-evolve. The circumvention of numerous strategies is more difficult than the circumvention of just one, especially if they are more effective together than either one by itself. Plant - herbivore co-evolution probably occurs through a series of feedback loops (Fox,1981; Rhoades,1985). Fox (1981) proposes two possible mechanisms:

1) Stepwise co-evolution:

This type of co-evolution occurs between specialist herbivores and unapparent plants. There is strong selection acting on the plant for it to be defended, while the herbivore adapts to continue consuming the plant. Polymorphic genes would ensure the rapid evolution of new defenses in the plant.

2) Diffuse herbivory:

Large apparent plants that are fed on by generalist herbivores are subject to different selection pressures from those mentioned above. With many herbivores there is little selective pressure applied by any one group. Natural selection favors broad spectrum defenses that are difficult to counter. These are deterrent rather than toxic to further reduce the selective pressures imposed on the herbivores. Complex polygenic control allows sufficient variability in the defenses to make these difficult to circumvent.

Most seaweed chemical defenses probably evolved in response to diffuse herbivory from generalist herbivores (Hay & Fenical,1988). Specialist herbivores are constrained by the necessity of finding their host seaweed. As most marine herbivores have planktonic larval stages, it is advantageous for these to be generalist herbivores upon settling. Larvae are subject to intense predation and are unlikely to be able to spend long periods of time searching for an appropriate host plant. Marine herbivores tend to have similar or longer generation times than their seaweed prey. Only a few have shorter generation times, as is typical in terrestrial systems. These are the mesograzers (Hay et al.,1988a; Hay & Fenical,1988). Some mesograzers (amphipods, isopods, and polychaetes) brood their young, thus avoiding the planktonic dispersal stage. This allows for greater specialization. However with their limited mobility mesograzers are restricted to well

defended apparent seaweeds that are often also widely distributed. Since these mesograzers appear to have a limited impact on plant fitness relative to the effects of larger fish and echinoids, the potential for true co-evolution is probably limited (Hay & Fenical, 1988). These constraints would not appear to promote co-evolution between herbivores and seaweeds in the marine environment.

5.0 SUMMARY

This essay summarizes strategies against generalist herbivores in marine macroalgae. Strategies may be classified into either escapes or defenses. Escape strategies include escapes in time, space, and rapid growth and size escapes. These strategies reduce the probability of a herbivore encountering the seaweed. Defenses can be either morphological or chemical. Defenses reduce the probability of tissue consumption, if the seaweed is encountered by a herbivore. Multiple defenses may occur in seaweeds in intensely grazed habitats like coral reefs.

Defenses, and probably also escapes, are presumably costly in terms of fitness to the seaweeds. However this cost should be less than that of tissue loss from grazing. A number of defense theories have arisen around the concept of costs and benefits. The Plant Apparency Model and Optimal Defense theory, the concept of induced defenses and the Resource Availability Hypothesis are discussed.

Strategies against herbivores probably evolved from existent adaptations allowing the seaweeds to survive in its environment. The co-evolution of herbivores and plants has been subject to different selection pressures in the marine environment compared to terrestrial systems.

Seaweeds are the simplest plants and so are ideal subjects for testing ecological theories, especially those that would be more difficult in larger, more complex terrestrial habitats. However none of the strategies outlined are generally applicable. They differ for each individual encounter between seaweed and herbivore. Herbivores differ in their mobility, sensory acuity, anatomy of the mouthparts, digestive processes, etc. Macroalgae vary in their apparency, defenses, nutritional quality, etc. It is likely that with this variability more strategies are likely to be recognized as our understanding of the marine environment increases.

6.0 REFERENCES

- Berner T. (1990) Coral reef algae. IN *Ecosystems of the World*. vol. 25 pp 253-264, (Z. Dubinsky, ed.), Elsevier, Amsterdam.
- Chew F.S. & Rodman J.E. (1979) Plant resources for chemical defense. IN *Herbivores: Their Interactions with Secondary Plant Metabolites*. pp 271-307, (G.A. Rosenthal & D.H. Janzen, eds.), Academic Press Inc. New York.
- Clayton M.N. (1990) The adaptive significance of life history characters in selected orders of marine brown algae. *Australian Journal of Ecology* 15:439-452.
- Coen L.D. & Tanner C.E. (1989) Morphological variation and differential susceptibility to herbivory in the tropical brown alga *Lobophora variegata*. *Marine Ecology Progress Series* 54:287-298.
- Coley P.D., Bryant J.P. & Stuart Chapin F. (1985) Resource availability and plant anti-herbivore defense. *Science* 230:895-899.
- Coley P.D. (1986) Costs and benefits of defense by tannins in a neotropical tree. *Oecologia* 70:238-241.
- Crawley M.J. (1983) *Herbivory: The dynamics of animal-plant interactions*. Blackwell Scientific, Oxford.
- Denton A., Chapman A.R.O. & Markham J. (1990) Size-specific concentrations of phlorotannins in three species of *Fucus*. *Marine Ecology Progress Series* 65:103-104.
- Feeny P. (1976) Plant apparency and chemical defense. *Recent Advances in Phytochemistry* 10:1-40.
- Fox L.R. (1981) Defense and dynamics in plant-herbivore systems. *American Zoologist* 21:853-864.
- Gaines S.D. & Lubchenco J. (1982) A unified approach to marine plant-herbivore interactions: II. Biogeography. *Annual Review of Ecology and Systematics* 13:111-138.
- Geiselman J.A. & McConnell O.J. (1981) Polyphenols in the brown algae *Fucus vesiculosus* and *Ascophyllum nodosum*: chemical defenses against the marine herbivore snail *Littorina littorea*. *Journal of Chemical Ecology* 7:1115-1133.
- Hay M.E. (1981) The functional morphology of turf forming seaweeds: persistence in stressful marine habitats. *Ecology* 62:739-750.
- Hay M.E. (1984) Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia* 64:396-407.
- Hay M.E. (1986) Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *American Naturalist* 128:617-641.

- Hay M.E., Duffy J.E. & Pfister C.A. (1987a) Chemical defense against different marine herbivores: are amphipods insect equivalents? *Ecology* 68:1567-1580.
- Hay M.E., Fenical W. & Gustafson K. (1987b) Chemical defense against diverse coral reef herbivores. *Ecology* 68:1581-1591.
- Hay M.E., Renaud P.E. & Fenical W. (1988a) Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. *Oecologia* 75:246-252.
- Hay M.E., Duffy J.E., Fenical W. & Gustafson K. (1988b) Chemical defense in the seaweed *Dictyopteris deliculata*: differential effects against reef fishes and amphipods. *Marine Ecology. Progress Series* 48:185-192.
- Hay M.E., Duffy J.E. & Fenical W. (1988c) Seaweed chemical defenses: among compound and among herbivore variance. *Proceedings of the 6th International Coral Reef Symposium*, 3:43-48.
- Hay M.E., Paul V.J., Lewis S.M., Gustafson K., Tucker J. & Trindell R.N. (1988d) Can tropical seaweeds reduce herbivory by growing at night? Diel patterns of growth, nitrogen content, herbivory and chemical versus morphological defenses. *Oecologia* 75:233-245.
- Hay M.E. & Fenical W. (1988) Marine plant-herbivore interactions: the ecology of chemical defense. *Annual Review of Ecology and Systematics* 19:111-145.
- Hay M.E., Pawlik J.R., Duffy J.E. & Fenical W. (1989) Seaweed herbivore predator interactions: host plant specialisation reduces predation on small herbivores. *Oecologia* 81:418-427.
- Hay M.E. (1991) Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. IN *The Ecology of Fishes on Coral Reefs*. Chp. 5, (P.F. Sale, ed.), Academic Press Inc., New York.
- Hay M.E. & Steinberg P.D. (1991) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. IN *Herbivores: Their Interactions with Secondary Plant Metabolites*, 2nd Ed. Vol. 2, pp 371-413. (Rosenthal G.E. & Berenbaum M.R., eds.), Academic Press Inc., San Diego.
- Horn M.H. (1989) Biology of marine herbivorous fishes. *Oceanography and Marine Biology Annual Review* 27:167-272.
- Iivessalo H. & Tuomi J. (1989) Nutrient availability and accumulation of phenolic compounds in the brown alga *Fucus vesiculosus*. *Marine Biology* 101:115-119.
- Johnson C.R. & Mann K.H. (1986) The importance of plant defense abilities to the structure of subtidal seaweed communities: the kelp *Laminaria longicuris* survives grazing by the snail *Lacuna vincta* at high population densities. *Journal of Experimental Marine Biology and Ecology* 97:231-267.
- Karban R., Brody A.K. & Schnathorst W.C. (1989) Crowding and a plant's ability to defend itself against herbivores and diseases. *American Naturalist* 134:749-760.

- Karban R. & Myers J.H. (1989) Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* 20:331-348
- Levin D.A. (1971) Plant phenols. *American Naturalist* 105:157-.
- Lewis S.M. (1985) Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia* 65:370-375.
- Lewis S.M., Norris J.N. & Searles R.B. (1987) The regulation of morphological plasticity in tropical reef algae by herbivory. *Ecology* 68:636-641.
- Littler M.M & Littler D.S. (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *American Naturalist* 116:25-44.
- Littler M.M, Littler D.S. & Taylor P.R. (1983) Evolutionary strategies in a tropical barrier reef. *Journal of Phycology* 19:229-237.
- Littler M.M, Taylor P.R. & Littler D.S. (1986) Plant defense associations in the marine environment. *Coral Reefs* 5:63-71.
- Littler M.M, Littler D.S. & Taylor P.R. (1987) Animal-plant defense associations: effects on the distribution and abundance of reef macrophytes. *Journal of Experimental Marine Biology and Ecology* 105:107-122.
- Lubchenco J. & Cubitt J. (1980) Heterotrophic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61:676-687.
- Lubchenco J. & Gaines S.D. (1981) A unified approach to marine plant-herbivore interactions: I. Populations and communities. *Annual Review of Ecology and Systematics* 12:405-437.
- McKey D. (1979) The distribution of secondary compounds within plants." IN *Herbivores: Their Interactions with Secondary Plant Metabolites*. pp 55-133, (G.A. Rosenthal & D.H. Janzen, eds.), Academic Press Inc., New York.
- Norris J.N. & Fenical W. (1982) Chemical defense in tropical marine algae. *Smithsonian Contributions to the Marine Sciences* 12:417-4 31.
- Norton T.A., Mathieson A.C. & Neushul M. (1982) A review of some aspects of form and function in seaweeds. *Botanica Marina* 25:501-510.
- Padilla D.K. (1985) Structural resistance of algae to herbivores. *Marine Biology* 90:103-109.
- Padilla D.K. (1989) Algal structural defenses: form and calcification in resistance to tropical limpets. *Ecology* 70:835-842.
- Paul V.J. (1985) Chemical adaptation in the pan-tropical green algae of the genus *Halimeda*. *Proceedings of the 5th International Coral Reef Symposium* 5:40-45.
- Paul V.J. & Hay M.E. (1986) Seaweed susceptibility to herbivory: chemical and morphological correlates. *Marine Ecology. Progress Series* 33:255-264.

- Paul V.J. (1987) Feeding deterrent effects of algal natural products. *Bulletin of Marine Science* 41:514-522.
- Paul V.J. & Fenical W. (1987) Natural products chemistry and chemical defenses in tropical marine algae of the phylum Chlorophyta. I N *Bioorganic Marine Chemistry*. vol.1 pp 1-30, (P.J. Scheuer, ed.), Springer Verlag, Berlin.
- Paul V.J., Wylie C.R. & Sanger H.R. (1988) Effects of algal chemical defense toward different coral reef herbivorous fishes: a preliminary study. *Proceedings of the 6th International Coral Reef Symposium* 3:73-78.
- Paul V.J. & van Alstyne K.L. (1988) Antiherbivore defenses in Halimeda. *Proceedings of the 6th International Coral Reef Symposium* 3: 133-138.
- The Pocket Macquarie Dictionary. (1989), (J.R.L. Bernard & D. Blain, eds.), Jacaranda Press, Sydney.
- Rhoades D.F. & Cates R. (1976) Toward a general theory of plant anti-herbivore chemistry. *Recent Advances in Phytochemistry* 10:168-213.
- Rhoades D.F. (1979) The evolution of chemical defense against herbivores. IN *Herbivores: Their Interactions with Secondary Plant Metabolites*. pp 3-54, (G.A. Rosenthal & D.H. Janzen, eds.), Academic Press Inc., New York.
- Rhoades D.F. (1985) Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *American Naturalist* 125:205-238.
- Steinberg P.D. (1984) Algal chemical defense against herbivores: allocation of phenolic compounds in the kelp, *Alaria marginata*. *Science* 223:405-407.
- Steinberg P.D. (1988) Effects of qualitative and quantitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. *Journal of Experimental Marine Biology and Ecology* 120:221-237.
- Steneck R.S. & Watling L. (1982) Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. *Marine Biology* 68:299-319.
- Steneck R.S. (1988) Herbivory on coral reefs: a synthesis. *Proceedings of the 6th International Coral Reef Symposium* 1:37-49.
- Swain T. (1979) Tannins and lignins. IN *Herbivores: Their Interactions with Secondary Plant Metabolites*. pp 657-682, (G.A. Rosenthal & D.H. Janzen, eds.), Academic Press Inc., New York.
- Tugwell S. & Branch G.M. (1989) Differential polyphenolic distribution among tissues in the kelps *Ecklonia radiata*, *Laminaria pallida* and *Macrocystis angustifolia* in relation to plant defense theory. *Journal of Experimental Marine Biology and Ecology* 129:219-230.

- van Alstyne K.L. (1988) Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. *Ecology* 69:6 55-663.
- van Alstyne K.L. (1989) Adventitious branching as a herbivore-induced defense in the intertidal brown alga *Fucus distichus*. *Marine Ecology Progress Series* 56:169-176.
- Watson D.C. & Norton T.A. (1985) The physical characteristics of seaweed thalli as deterrents to littorine grazers. *Botanica Marina* 28:383-387.
- Zucker W.V. (1983) Tannins: does structure determine function? An ecological perspective. *American Naturalist* 121:335-365.