



## Paradigm lost: reconsidering functional form and group hypotheses in marine ecology

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### Abstract

Although functional form and functional group models for marine algae have been used extensively, there is little general literature support for these models, and many studies have shown that associated hypotheses are often incorrect. In functional form/group models, a wide range of ecological and physiological functions are assumed to be correlated with general algal form or morphology. In contrast, functional group approaches have been used most successfully in terrestrial and aquatic systems when groupings are based on a particular function rather than overall plant morphology, and when addressing ecosystem-level questions. In this type of functional group approach, a given set of species would likely be grouped differently depending on the function under consideration. Functional groupings are appropriate for many situations and questions, but not all. Certainly, grouping taxa by a particular function can be very useful and often necessary for many ecosystem-level questions and modeling, especially where qualitative results are more important than quantitative predictions, and when there are too many species in a system to consider them all individually. However, when one considers species–species interactions or questions about population biology, the specific responses of individual species must be considered. To make functional group models more useful, we recommend that groupings be based on specific functions (e.g. nutrient uptake rates, photosynthesis rates, herbivore resistance, disturbance resistance, etc.) rather than gross morphology. Explicit testing of performance of a particular function should be made before generalizations can be assumed, and groupings should be used for questions/approaches where they are most appropriate. If models fail when tested, they should be modified using the additional information to generate new hypotheses and models, and then retested. © 2000 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

In all of ecology, we strive to find overriding, generalizing principles. General models of behaviors of systems and species would be very useful for allowing us to both explain observed patterns in nature, as well as predict future patterns. Some of the most encompassing models for marine ecology are those that deal with the form of marine plants, primarily algae.

Marine plants are the major structural components of many communities, and can create habitats for animals and protect them from predators, desiccation, or water motion. Plant morphology can directly influence the ability of herbivores to consume tissue by affecting handling or consumption (Padilla, 1984, 1985, 1987). In addition, plant surface area, stature and form can influence area for light reception, nutrient uptake, and gas exchange, as well as the impact and magnitude of hydrodynamic forces experienced in marine environments (Denny et al., 1985; Duffy and Hay, 1991; Holbrook et al., 1991; Cecchi and Cinelli, 1992; Denny, 1995; Gaylord and Denny, 1997).

Plant form can be considered at several different scales, from the overall gross morphology of the plant, to cellular arrangement, to the component chemicals of cellular construction. The physical properties of plant form can be decomposed into those that are a result of the overall structure of the plant, or structural properties, and the material properties of the cells and other microscopic components of the plant. Structural properties include gross morphology, form and construction (Gordon, 1968; Leicester, 1973). For example, different types of materials are used to construct a house: wood, concrete, brick. These materials are combined in different ways to create the overall structure of a house (e.g. concrete is used for the foundation, wood in various forms is used for the frame, etc.). Material properties include cell structure, chemical composition of cell wall materials, cell organization, fibers, and mineralization (Wainwright et al., 1976; Vincent, 1982; Vogel, 1988). Both material and structural properties affect the ability of a plant to resist consumers, just as the materials and structural properties of a house affect its structural strength and mechanics (Gurfinkel, 1981). Similarly, the mechanical properties and dynamics of use of a herbivore's feeding apparatus will influence its ability to consume the tissue of a given plant (Padilla, 1985, 1987, 1989).

Little and Little (1980) proposed a model where the overall form of an alga was hypothesized to predict many aspects of its physiology and ecology, including resistance to consumers. A similar model was proposed by Steneck and Watling (1982). They hypothesized that form and mineralization of algae dictated resistance to consumption by grazers, in particular molluscs. Although these two hypotheses differ slightly in detail, overall they are very similar. These models are called functional group or functional form models, however, groupings are based on gross form or morphology, with which function is only inferred or assumed to be correlated. The general models hypothesize that algal growth form and mineralization dictate relative rates of primary productivity, growth rate, competitive ability, resistance to herbivores, resistance to physical disturbance, tolerance to physiological stress, and successional stage, and that all of these functions are correlated with each other. Function is one of those terms that has many different meanings, and in science has been used in a variety of ways (Wright, 1973). In

some cases we refer to the role or effect of a species in a system as its function. At other times we are concerned with how a species performs, or functions, under different circumstances (Cummins, 1975). Scientists have not generally been explicit in defining the terms function or functional, which when used can often lead to confusion and a blurring of meaning, as is the case of functional form and functional group models.

In the Littler and Littler (1980) model, algae are placed into one of several form groups: sheet, filamentous, coarsely branched, thick leathery, jointed calcareous, and crustose. These form groups are hypothesized to represent the rank order of a wide variety of traits of algae, including: decreasing maximum photosynthesis rates, decreasing nutrient uptake rates, decreasing susceptibility to herbivores, decreasing susceptibility to physical stress, decreasing susceptibility to physiological stress, increasing competitive ability, and increasing successional stage. The Steneck and Watling (1982) model is very similar, but creates slightly different ranked form groups: filamentous, foliose, corticated, leathery, articulated calcareous, and crustose.

## 2. Support for the functional form/group models

Although these hypotheses seem to have been generally accepted, for example, they are presented in text books as fact (Lobban and Harrison, 1994), there is at best mixed empirical support for these models. We searched the literature published between January 1980 and December 1999 (Science Citation Index) for all papers that referenced Littler and Littler (1980) (250 + papers in 55 journals; many of these papers also cited Steneck and Watling, 1982). We examined in detail all of the papers that appeared in the journals *Ecology*, *Journal of Experimental Marine Biology and Ecology*, *Journal of Phycology*, *Marine Biology*, *Marine Ecology Progress Series*, and *Oecologia* (142 articles, representing > 50% of the total; these journals were chosen because they are more likely to publish experimental studies). The 49 studies that provided experimental tests of the functional form/group models were classified as either supporting or not supporting the relevant model predictions, based on the authors' overall interpretation of their data (Table 1).

Many studies found that primary productivity (photosynthesis and nutrient uptake rates) correlated well with algal morphology. In contrast, most studies addressing hypotheses of susceptibility to herbivores, tolerance to physiological stress, or relative successional stage found little support for the functional form/group models. In some studies that reported support for the models (e.g. Littler and Littler, 1984; Littler et al., 1987), the authors found species which did not conform to the general patterns.

Consistent support is clearly lacking for many of the predictions of these models. Although one might argue that data that falsify the models are more likely to be reported than are data that support them (notwithstanding the 20 + articles relating to primary productivity), there are enough negative results to call into question the generality of the functional form/group approach. A problem not explicitly addressed in most of the above studies is the potentially high morphological and ecological variability within a functional group or even a single species (Gerard and Mann, 1979; Armstrong, 1987, 1989; Gerard and DuBois, 1988; Coen and Tanner, 1989; Carrington, 1990). For

Table 1

Summary of 49 articles from six journals<sup>a</sup> citing Littler and Littler (1980), in which the authors conducted experiments and explicitly discuss their results with respect to the predictions of algal functional form/group models; cell values are the number of studies that either showed support or no support

Hypothesis	Support <sup>b</sup>	No support <sup>b</sup>
Primary productivity		
Photosynthesis rate	18 <sup>1–18</sup>	2 <sup>19, 20</sup>
Nutrient uptake	8 <sup>15, 21–27</sup>	NR
Resistance to herbivores	6 <sup>4,5,7<sup>c</sup>,8,28,29</sup>	11 <sup>30–40</sup>
Tolerance to physiological stress	NR	1 <sup>41</sup>
Successional stage	4 <sup>1,4<sup>d</sup>,42,43</sup>	8 <sup>7, 18, 44–49</sup>

<sup>a</sup> Ecology, Journal of Experimental Marine Biology and Ecology, Journal of Phycology, Marine Ecology Progress Series, Oecologia.

<sup>b</sup> Superscripts indicate references. NR = none reported. 1, Littler and Littler, 1981; 2, Fain and Murray, 1982; 3, Littler and Arnold, 1982; 4, Littler and Littler, 1983; 5, Littler et al., 1983a; 6, Oates and Murray, 1983; 7, Littler and Littler, 1984; 8, Littler et al., 1987; 9, Hanisak et al., 1988; 10, Peckol and Ramus, 1988; 11, Zupan and West, 1990; 12, Enriquez et al., 1994; 13, Geertzhansen et al., 1994; 14, Enriquez et al., 1995; 15, Rivers and Peckol, 1995; 16, Enriquez et al., 1996; 17, Gacia et al., 1996; 18, Weykam et al., 1996; 19, Oates, 1985; 20, Matta and Chapman, 1991; 21, Rosenberg et al., 1984; 22, Wallentinus, 1984; 23, Ramus and Venable, 1987; 24, Duke et al., 1989; 25, Hein et al., 1995; 26, Pedersen and Borum, 1996; 27, Pedersen and Borum, 1997; 28, Horn et al., 1982; 29, Taylor et al., 1986; 30, Hay, 1984; 31, Padilla, 1985; 32, Coen, 1988; 33, Coen and Tanner, 1989; 34, Padilla, 1989; 35, Arrontes, 1990; 36, Duffy and Hay, 1991; 37, Winter and Estes, 1992; 38, Wakefield and Murray, 1998; 39, Iken, 1999; 40, Overholtzer and Motta, 1999; 41, Dudgeon et al., 1995; 42, Littler et al., 1983b; 43, Duggins and Dethier, 1985; 44, Dethier, 1981; 45, Vandermeulen and DeWreede, 1986; 46, Davis and Wilce, 1987; 47, Cecchi and Cinelli, 1992; 48, Phillips et al., 1997; 49, Airoldi, 1998.

<sup>c</sup> *Dictyota dichotoma* does not fit the predictions of the model.

<sup>d</sup> Crustose ralfsoid form of *Scytosiphon lomentaria* does not fit the predictions of the model.

example, Kilar et al. (1989) found significant differences in photosynthesis rates among phenotypically distinct morphs of the alga *Sargassum polyceratum*. In a very thorough and elegant study, Dethier (1994) found that different species of encrusting algae (a single functional group) exhibit substantial variability with respect to herbivore resistance, tolerance to physiological stress, and life history. In addition, the definitions of functional groups can be ambiguous when actually applied to real species. Phillips et al. (1997) found that 14 of 82 algal species in their system did not clearly fall into any one functional group. They also noted that in other studies the assignment of certain species to a given group varied, even when considering those studies conducted by the same researchers.

### 3. Other considerations

Lack of empirical support for these models may be understood by examining other factors that influence the processes under consideration. If we focus on one aspect in particular, the prediction of resistance to herbivores, it is easy to see why these hypotheses may not be generally true. Factors known to be important in marine

plant–herbivore interactions that are not necessarily correlated with plant form include food quality (Jernakoff et al., 1996), defensive chemistry (reviewed in Hay and Fenical, 1988), and phenotypic plasticity (VanAlstyne, 1988a, 1989; Cronin and Hay, 1996a). Defensive chemistry has been particularly well studied in marine systems, and an impressive array of diverse chemicals has been found in all types and forms of algae (Targett et al., 1986; Paul and VanAlstyne, 1992; Hay, 1996; Cronin et al., 1997). These chemicals are important deterrents of feeding by a wide range of herbivores, and have proven to inhibit epiphytes, parasites, and microbial activity as well (Steinberg, 1986). Grazing by herbivores has also been demonstrated to induce phenotypically plastic morphological and structural changes in some algae, as well as increases in defensive chemistry (VanAlstyne, 1988b; Lowell et al., 1991; Cronin and Hay, 1996b,c).

Other important considerations are the mechanical properties of algae (Koehl, 1986; Denny et al., 1989). Although the functional form/group models confound material and structural properties with overall morphology, these properties of plants are a critical part of resistance to any type of disturbance, be it herbivores or physical disturbance (Biedka et al., 1987; Gaylord et al., 1994; Friedland and Denny, 1995; Shaughnessy et al., 1996). We know that both materials and structures have different mechanical properties when forces are applied to them in different ways (e.g. compression, tension, bending, abrasion; Gordon, 1968; Wainwright et al., 1976; Vincent, 1982). For example, concrete is very strong in compression ( $36.5 \text{ MN m}^{-2}$ ), but much weaker in tension ( $2.9 \text{ MN m}^{-2}$ ), and both the compressive and tensile strength of concrete can be greatly increased if it is mixed with other materials ( $140 \text{ MN m}^{-2}$  in compression,  $11 \text{ MN m}^{-2}$  in tension) (Vincent, 1982; Gibson, 1994). The same will be true for marine plants whose tissue and thalli are constructed of a variety of materials and structural elements arranged in different ways (Koehl and Wainwright, 1977; Koehl, 1986; Biedka et al., 1987).

Mechanical, material and structural factors all interact to affect the different ways plants may be damaged by the feeding of various herbivores (Parker et al., 1993; Parker and Chapman, 1994). Marine herbivores can bite with jaws and teeth (e.g. fish and echinoids), cut or tear (e.g. crustacean chelae, jaws), or rasp or abrade algae (e.g. molluscan radulae). Marine herbivores not only vary considerably in how they feed, but also in their absolute size, and their size relative to the plant they are eating. The size scale of an herbivore and its feeding apparatus relative to the structural elements of a plant will influence the relative importance of material and structural properties, as well as which particular structural properties are important (Leicester, 1973). For example, plant material properties may be much more important than overall form for micrograzers (1–5 mm) feeding on macrophytes, while the relative importance of material or structural properties will depend on the size of the macrophyte for mesograzers (5–40 mm). Both materials and structure of the plant will be important for mesograzers feeding on filamentous algae, but structural construction will be much less important than the material properties of the thallus for grazers on large kelp. In addition to the wide range of sizes of marine grazers, marine plants can span more than an order of magnitude in size within some functional/form groups (Johnson and Koehl, 1994).

Grazer preferences are often used to infer relative mechanical susceptibility of marine plants to herbivores, however, preferences can be influenced by food quality, chemistry,

nutritional status of the herbivore, and a variety of other factors. To circumvent these difficulties, Padilla (1984, 1989) used the actual functioning of the feeding apparatus of one important type of grazer, limpets, and directly tested the susceptibility to tissue loss of algae grouped by plant form and degree of calcification as defined by the form/group models. She found that for five species of limpets and seventeen species of algae, the resistance of the algae to grazer damage was the opposite of that predicted by the models. Other experiments with an herbivorous crab and fish also found no support for the form/group hypotheses (Padilla, 1987). Padilla (1993) suggested an alternative hypothesis to explain the importance of form and mineralization in marine macrophytes, particularly in reducing the loss of tissue subsequent to mechanical damage. This work clearly demonstrates that if we choose different performance criteria (e.g. resistance to tissue loss to grazing limpets versus resistance to tissue loss subsequent to herbivore damage) algae could be aligned in different groups with correspondingly different relative rankings.

Other factors in addition to nutritional, chemical, and mechanical features of algae may also affect the properties of macrophytes and must be considered (Bell, 1993, 1995). Phylogenetic relatedness has recently been shown to be very important for all areas of comparative and functional biology (Felsenstein, 1985; Starck, 1998 and references therein). Closely related species might be predicted to have more similar features in addition to morphology, than more distantly related species. This lack of independence due to a shared phylogenetic/evolutionary history means that generalizable tests of correlation between form or morphology and specific functions must either take evolutionary relatedness into account statistically (Felsenstein, 1985), or should only include very distantly or unrelated taxa. For example, all temperate calcified algae are in a single family, Corallinacea. Correlations of mineralization and specific functions of calcified algae should therefore include tropical algae, where many different, unrelated taxa are all calcified (Borowitzka, 1982; Hay, 1984; Padilla, 1987, 1989).

Plants also respond physiologically and morphologically to environmental factors. Physiological rates such as photosynthesis and nutrient uptake can be affected by desiccation, light levels, heat, and nutrient delivery rates, among others (Gerard, 1982; Murthy et al., 1987; Koehl and Alberte, 1988; Williams and Carpenter, 1988; Bell, 1993, 1995). Within functional groups, and even within species, these physiological rates will vary considerably, depending on local environmental conditions, either through genetically different ecotypes or through phenotypically plastic responses of individuals (Gerard and Mann, 1979; Rice et al., 1985; Kilar et al., 1989; VanAlstyne and Paul, 1990; Arnold et al., 1995). Similarly, plant form and mechanical properties are affected by and respond to water motion and hydrodynamic stresses as well as damage by herbivores (Gerard, 1987; Kraemer, 1990; Kraemer and Chapman, 1991; Lowell et al., 1991).

Steneck and Dethier (1994) proposed another functional group model to predict the structure of algal dominated communities based on environmental parameters. Their model predicted general patterns of distribution of functional form grouping of algae (micro, filamentous, foliose, corticated, leathery, articulated calcified, and crustose algae) along gradients of productivity and disturbance potential. They assumed that physical disturbances will act similarly to herbivores, and have a similar frequency and intensity as herbivore disturbance.

They presented information from three different systems (intertidal and subtidal rocky shores in Maine, intertidal rocky shores in Washington, and subtidal reef communities in the Caribbean) to produce a general hypothesis. Although they did not claim that the data from these three systems provided a test or proof of their model, the model does not adequately describe the patterns of algal group abundance at any of the three sites. For example, the general model predicts a uniform abundance of crustose algae across all types of habitats, which is not seen at any specific site. Leathery macrophytes are predicted to be dominant only at the most productive, least disturbed habitats, however, they are absent from the tropical site, and most abundant in other habitats in the two temperate sites. A similar lack of concordance can be found for other groups.

This model was directly tested by Phillips et al. (1997), in western Australia, who found no support for the relevant predictions. The responses of individual species were often the most dramatic, and did not always correspond to the responses of their assigned functional group. In addition, they found it difficult to assign species to the functional groups; > 15% could not be readily categorized.

#### **4. New directions**

Given all of the problems that seem to be apparent with current form group/functional group models for marine plants, why have they seemingly become paradigm? As was noted by DeBeer (1958) when considering the often used phrase ontogeny recapitulates phylogeny, “It is characteristic of a slogan that it tends to be accepted uncritically and dies hard”. Certainly it is very desirable to be able to group taxa to facilitate making generalizations, when species are numerous and identifications are difficult, and when we are modeling systems. Indeed, functional group models have been used with some success in other systems. For example, terrestrial ecologists have used functional groups to address many questions (Schulze and Mooney, 1994, and references therein). There are important differences, however, in how functional groups have been used in terrestrial versus marine systems. In terrestrial systems, groupings are based on a specific function, and species are distributed to groups based on that functional criterion. For example, life form, type of life history, overall size, leaf structures, rooting depth, symbiotic associations, gas exchange characteristics, photoperiodic sensitivity, and fire resistance are all factors for which functional groupings have and can be defined (Körner, 1994). Groupings may be defined by different quality criteria (structure, physiology, life history), spatial arrangement (horizontal or vertical distribution), or temporal appearance or activity (early successional versus late successional, winter versus summer annuals, annuals versus perennials). When a different function is considered, the same species might well be assigned to very different groups. This is in contrast to marine systems where species are assigned to groups solely on the basis of form, and function is inferred, and all functions are assumed to similarly correlate with form.

Clearly there are circumstances and questions where a functional grouping approach would be very useful in marine systems, however, this methodology is not appropriate for all questions of scientific interest. For example, questions of species specific processes that require knowledge about how a given species performs or responds (e.g.

population growth rate, life history) do not lend themselves to a grouping approach (Körner, 1994; Iken, 1999). Likewise, when addressing species–species interactions (e.g. herbivore preferences, mutualistic associations) the properties of individual species will be most important, and it is unlikely those properties will be generally shared with other plants of the same gross form (Iken, 1999). In some cases groupings may be useful for community level questions (e.g. succession), while in others they are not (e.g. species diversity and richness, food web interactions). Groupings may be the most useful at the ecosystem level, particularly in modeling ecosystem processes. Models of ecosystem processes generally cannot include all species within a system, and generalizations and simplifications can facilitate our ability to follow and understand processes at this level (Carpenter, 1988).

An excellent example of a functional group approach that appears to work well is the study of microalgal turfs on tropical reefs. This group is composed of a very large number of species of unicellular and filamentous algae from five major divisions (Williams and Carpenter, 1990). Williams and Carpenter (1990) experimentally demonstrated that knowledge of individual species identity was not necessary to estimate photosynthesis and photon flux density relationships in this assemblage. Other studies have considered carbon flux, nitrogen flux and other factors that are all important for understanding ecosystem processes in this system (Williams and Carpenter, 1990, 1997, 1998; Carpenter and Williams, 1993). Indeed, the functional form/group models seem to reasonably describe physiological processes that, in aquatic systems, may be dependent on morphological relationships such as surface area to volume ratio. However, although scientists studying reef communities have a very specific definition for the group ‘turf’, it is worth noting that this same term has been used by numerous other scientists to describe everything from micro algae to large bladed algae (Table 2).

One area where form groups as suggested by Littler and Littler (1980) and Steneck and Watling (1982) may be useful is when the function of interest is determining structure/habitat for other organisms. The overall form and three dimensional structure of a plant will influence its ability to provide habitat for animals of different sizes (Gosselin and Chia, 1995), affect water motion (Denny et al., 1985; Denny, 1995), and reduce desiccation (Padilla, 1984).

Many studies have found that macroalgal ‘turfs’ provide important habitat for animals, and increase local community richness (Whorff et al., 1995; Taylor, 1998; Aseltine-Neilson et al. 1999).

Table 2

The Term ‘turf’ is used to describe a variety of algal communities; we searched Science Citation Index for all references published from 1978 to 1999 using the key phrase ‘alga\* turf\*’. Our search found 89 papers, 71 of which we had access to. These papers were in 27 journals (12 with > 1 paper)

General description of species in group	Number of papers
Microscopic filamentous	10
Articulated coralline	9
Medium-sized branched or bladed	32
Mixed (microscopic and macroscopic)	11
Unidentified	9



## 5. Conclusions

In all areas of ecology, we are striving to find and develop generalizable principles. Generalizations can be essential for studying complex systems, or when addressing complex questions. The development of verbal models, such as those of Littler and Littler (1980), Steneck and Watling (1982), and Steneck and Dethier (1994) can be useful tools for formulating such generalizations. These models are the first step in hypothetico–deductive reasoning promoted by Popper as the best approach to the scientific method (in Miller, 1994). However, the development of such hypotheses is only the first step. According to Popper, once hypotheses are erected, they must be tested. If the models are not supported by the tests, then we should use the new information that is gained to change or modify our models, and generate new hypotheses for testing. With increasing repetition of this process, both our knowledge and science will progress (Mentis, 1988).

Although Popper's philosophy of science is generally considered the most appropriate model, Platt (1964) has argued for the systematic application of what he calls strong inference. Rather than considering single hypotheses, Platt promotes the initial consideration of all alternative hypotheses to explain a question of interest. In strong inference, the following steps are applied: (1) devise alternative hypotheses, (2) devise crucial experiments with alternative possible outcomes that will, as nearly as possible, exclude multiple hypotheses and (3) carry out experiments to get clean results. This procedure is recycled, making sub- or sequential hypotheses to refine the possibilities that remain. By rigorous application of this cyclic procedure, Platt suggests that science should progress most rapidly. We suggest that the use of strong inference is the most effective way to approach complex questions about the importance of form and structure of marine algae in ecological systems.

Current functional form/group hypotheses regarding many aspects of the ecology of marine algae do not appear to be supported by the data. Alternative hypotheses should be erected and directly tested. Although we may not find all-encompassing explanations, in many cases, we might identify broadly applicable factors, such as the importance of anti-herbivore chemistry in influencing herbivore preference for many algal species. Some aspects of the functional form/group models may be robust, particularly those that relate physiological processes to form.

However, an alternative hypothesis for the correlation of form/groups with photosynthesis and nutrient uptake rates may be that these processes are directly related to total plant surface area or surface area to volume ratios (Enriquez et al., 1996). If either of these hypotheses is true, then accepting the most parsimonious explanation would not necessitate invoking form/group models.

These and other alternative hypotheses should be directly tested relative to the form/group models. More useful functional group models may be developed if they are based on specific functions, which have been explicitly and rigorously tested. It is important to consider the most appropriate scales at which to evaluate properties. In addition, it is important to consider other factors that will influence the properties under consideration, including evolutionary history and relatedness, phenotypic and genetic variability, chemistry, physiology, and mechanics.

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