

THE EVOLUTION OF THALLUS FORM AND SURVIVAL
STRATEGIES IN BENTHIC MARINE MACROALGAE:
FIELD AND LABORATORY TESTS OF A FUNCTIONAL FORM MODEL

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Morphological attributes of algae have long been considered primarily from the standpoint of taxonomy and used to discover new species or to speculate on phylogenetic affinities. While these approaches are of value, a fresh outlook that synthesizes the adaptational significance of algal structure, ecology, and physiology is needed.

Very few studies have considered algal structure and its relationship to primary productivity. Odum et al. (1958) reported the uptake of ^{32}P as well as primary productivity to be correlated with calculated surface to volume ratios for seven marine algae. Kanwisher (1966) viewed the algal thallus as a population of photosynthetic cells in a structural matrix; he noted that massive forms, containing relatively higher ratios of structural to photosynthetic components, tended to have a lower photosynthetic capacity than more delicate species. Littler (1979) found a close relationship between thallus (i.e., morphological) form and light-saturated photosynthetic rates for 45 species of marine macroalgae. Additionally, the high productivity of seaweeds has been emphasized by Mann (1973) and discussed in view of several postulated growth strategies.

A major limitation of the traditional productivity approach to ecological research has been the emphasis placed on describing photosynthetic and respiratory features for producer populations, which thus far has provided little information on the important selective processes that determine these properties. This focus, while giving useful specific and detailed data, has not added greatly to the ability to make predictions or general statements. Clearly, a costs versus benefits approach relating the diverse features of algal morphology to ecological interactions (e.g., succession, competition, predation) and physiological functions (e.g., primary productivity and respiration) is needed to assess important adaptational strategies. The present research explores the general concept that morphology, ecological attributes, and productivity are interrelated and synthesizes the adaptive significance of thallus form relative to the productivity ecology and survival of benthic macroalgae.

Two procedures were used to evaluate costs and benefits: (1) manipulative experiments of succession and (2) empirical tests of hypothetical strategies for

seral sequences in macrophyte succession. This latter method can be used only if the initial hypotheses are posed properly; a critical problem is the intuitive formulation of appropriate survival strategies.

The evolution of environmental resistance (hardiness), defenses against predation, and interference competition may well involve costs because of: (1) an energetic commitment; (2) a material commitment that might result in reduced potential for new growth and reproduction; as well as (3) the possible incompatibility of such resistance or defensive systems with basic physiological processes. For a given feature to be selected, the benefits resulting from the required investment of resources must be greater than the competing alternative investments that are possible within the organisms' genetic limitations. In general, the following three overall features should pertain in regard to marine macroalgal energetics.

1. Marine macroalgae have basic energy requirements; energy used for environmental resistance or morphological defensive systems is not available for other uses. (However, evidence exists that some chemical defense compounds also function in primary processes [Seigler and Price 1976; Seigler 1977].)

2. The relationship between production rates and morphology for algal communities from different habitats should be similar in the absence of major environmental constraints if ecological pressures on various morphological/physiological types act as widespread selective forces.

3. Different algae may adapt to similar environments through different evolutionary channels (imposed by previously acquired genetic information which cannot be modified drastically in a short time) in a divergent (not convergent) manner, thus resulting in both spatial and temporal partitioning of resources.

Testable hypotheses were formulated by considering the kinds of selective pressures on algal species from early successional seres (characteristic of disturbed environments; Connell 1975; Murray and Littler 1978) in comparison to those on algae from intermediate and mature communities (typical of nonstressful habitats). From these considerations, the extremes of a broad range of adaptive features for various kinds of seaweeds could be postulated and tested.

METHODS AND MATERIALS

The evolutionary history of macroalgae has resulted in a great diversity of metabolic responses and thallus forms. These physiological and morphological adaptations must reflect different survival strategies in terms of trade-offs between capacities for rapid growth, reproduction, environmental tolerance, resistance to predation, competition (for nutrients, space, and light), and perhaps in some cases cooperative interactions (e.g., mutualism). However, it must be kept in mind that at different stages in the life history of a given species it is highly likely that strategies might change (e.g., crust versus upright bladeliike alternants in *Scytosiphon*, *Petalonia*, and *Gigartina*; small sheetlike thalli versus large differentiated thalli in juvenile and mature kelps).

Opportunistic macroalgae, because of the relative unpredictability (e.g., temporal and spatial variability) and other constraints of their environment, hypothetically should possess the strategies outlined on the left in table 1 along

TABLE 1

HYPOTHETICAL (a priori) SURVIVAL STRATEGIES AVAILABLE TO OPPORTUNISTIC
MACROALGAE REPRESENTATIVE OF STRESSED* COMMUNITIES VERSUS
MACROALGAE CHARACTERISTIC OF NONSTRESSED† COMMUNITIES

Opportunistic Forms	Late Successional Forms
1. Rapid colonizers on newly cleared surfaces	1. Not rapid colonizers (present mostly in late seral stages), invade pioneer communities on a predictable seasonal basis
2. Ephemerals, annuals, or perennials with vegetative short-cuts to life history	2. More complex and longer life histories, reproduction optimally timed seasonally
3. Thallus form relatively simple (undifferentiated), small with little biomass per thallus; high thallus area to volume ratio	3. Thallus form differentiated structurally and functionally with much structural tissue (large thalli high in biomass); low thallus area to volume ratio
4. Rapid growth potential and high net primary productivity per entire thallus, nearly all tissue photosynthetic	4. Slow growth and low net productivity per entire thallus unit due to respiration of non-photosynthetic tissue and reduced protoplasm per algal unit
5. High total reproductive capacity with nearly all cells potentially reproductive, many reproductive bodies with little energy invested in each propagule; released throughout the year	5. Low total reproductive capacity, specialized reproductive tissue with relatively high energy contained in individual propagules
6. Calorific value high and uniform throughout the thallus	6. Calorific value low in some structural components and distributed differentially in thallus parts. May store high-energy compounds for predictable harsh seasons
7. Different parts of life history have similar opportunistic strategies, isomorphic alternation, young thalli just smaller versions of old	7. Different parts of life history may have evolved markedly different strategies, heteromorphic alternation, young thalli may possess strategies paralleling opportunistic forms
8. Escape predation by nature of their temporal and spatial unpredictability or by rapid growth (satiating herbivores)	8. Reduce palatability to predators by complex structural and chemical defenses

* Young or temporally fluctuating.

† Mature, temporally constant.

with the concomitant costs and benefits put forth in table 2. Such costs and benefits represent measurable attributes whose presence might identify selective forces directing the proposed evolutionary pathways.

Selective factors prevalent in mature, temporally constant communities (e.g., in response to greater environmental predictability and associated increased biological pressures) would be expected to favor the strategies that are presented on the right in table 1, with their accompanying measurable cost/benefit attributes (outlined in table 2) used to test the various strategies. It is appreciated that the features given in tables 1 and 2 represent the extreme ends of a continuum and, also, that many algal species' life histories include markedly different thallus forms having concomitantly different environmental resistances, growth rates, and reproductive capacities. However, these points in no way lessen the value of the hypothesized strategies and costs/benefits (tables 1 and 2) as a framework for examining the role of critical selective forces. The reliability of several of the predictions was assessed by directly measuring physiological, calorific, morpho-

TABLE 2
 HYPOTHETICAL COSTS AND BENEFITS OF THE SURVIVAL STRATEGIES PROPOSED
 IN TABLE 1 FOR OPPORTUNISTIC (INCONSPICUOUS) AND LATE
 SUCCESSIONAL (CONSPICUOUS) SPECIES OF MACROALGAE

Opportunistic Forms	Late Successional Forms
COSTS	
<ol style="list-style-type: none"> 1. Reproductive bodies have high mortality 2. Small and simple thalli are easily outcompeted for light by tall canopy formers 3. Delicate thalli are more easily crowded out and damaged by less delicate forms 4. Thallus relatively accessible and susceptible to grazing 5. Delicate thalli are easily torn away by shearing forces of waves and abraded by sedimentary particles 6. High surface to volume ratio results in greater desiccation when exposed to air 7. Limited survival options due to less heterogeneity of life history phases 	<ol style="list-style-type: none"> 1. Slow growth, low net productivity per entire thallus unit results in long establishment times 2. Low and infrequent output of reproductive bodies 3. Low surface to volume ratios relatively ineffective for uptake of low nutrient concentrations 4. Overall mortality effects more disastrous because of slow replacement times and overall lower densities 5. Must commit a relatively large amount of energy and materials to protecting long-lived structures (energy that is thereby unavailable for growth and reproduction) 6. Specialized physiologically and thus tend to be stenotopic 7. Respiration costs high due to maintenance of structural tissues (especially during unfavorable growth conditions)
BENEFITS	
<ol style="list-style-type: none"> 1. High productivity and rapid growth permits rapid invasion of primary substrates 2. High and continuous output of reproductive bodies 3. High surface to volume ratio favors rapid uptake of nutrients 4. Rapid replacement of tissues can minimize predation and overcome mortality effects 5. Escape from predation by nature of their temporal and spatial unpredictability 6. Not physiologically specialized and tend to be more eurytopic 	<ol style="list-style-type: none"> 1. High quality of reproductive bodies (more energy per propagule) reduces mortality 2. Differentiated structure (e.g., stipe) and large size increases competitive ability for light 3. Structural specialization increases toughness and competitive ability for space 4. Photosynthetic and reproductive structures relatively inaccessible and resistant to grazing by epilithic herbivores 5. Resistant to physical stresses such as shearing and abrasion 6. Low surface to volume ratio decreases water loss during exposure to air 7. More available survival options due to complex (heteromorphic) life-history strategies 8. Mechanisms for storing nutritive compounds, dropping costly parts, or shifting physiological patterns permit survival during unfavorable but predictable seasons

logical, palatability, and physical qualities of macroalgae from various successional seres during laboratory and field experiments.

Successional data.—Experimental succession plots were permanently marked and sampled for percent cover using the methods described by Littler (1980). The plots were clustered as four disturbed 0.15 m² quadrats within a 0.6 by 1.0 m perimeter located in the interval between +0.15 and +0.45 m (relative to mean lower low water, MLLW) in an undisturbed rocky intertidal community located on San Clemente Island, California. The experiment was begun (December, 1974) by manually removing all biota followed by ethanol and flame sterilization. Subsequent successional events were recorded and analyzed photographically for the next 12 mo. Additional successional data were obtained (Murray and Littler, in press) using cleared but unsterilized substrata throughout the intertidal on Santa Catalina Island, California. From the results of these manipulations (fig. 1), the following five macroalgae were selected as representative of a spectrum of seral stages: *Ulva* sp. (pioneer species), *Gelidium purpurascens/robustum* and *Egregia menziesii* (intermediate to later seral species), *Corallina officinalis* (climax species), and *Pelvetia fastigiata* (upper intertidal climax species). Representative thallus forms and sizes of these algae are illustrated in fig. 2. *Gelidium purpurascens/robustum* represented a single entity that could not be reliably placed in either *G. purpurascens* or *G. robustum* because its morphology was intermediate between these highly similar species (see Abbott and Hollenberg 1976, p. 349). All five taxa were then examined experimentally from the viewpoints outlined in tables 1 and 2 as follows.

1. *Productivity hypothesis.*—The opportunistic species (e.g., *Ulva* sp.) should show higher net productivity values than the climax species (e.g., *C. officinalis* and *P. fastigiata*) if selection has favored rapid growth in unpredictable environments. Intermediate seral macrophytes (e.g., *E. menziesii* and *G. purpurascens/robustum*) should show intermediate values.

2. *Maintenance-costs hypothesis (reciprocal of the productivity hypothesis).*—Net photosynthesis per unit of total thallus weight should be relatively low in algae from subclimax and climax communities characteristic of predictable environments, if selection has acted to favor organisms that allocate resources for environmental resistance, interference competition, and anti-predator defenses having large proportions of respiratory or nonmetabolic structure (with high initial energy costs).

Measurements of net photosynthesis were made for the five experimental macroalgae (four replicates each) on San Clemente Island between 0900 and 1400 h during May, 1975, at 16.0° C under overcast skies of about 44 klx. Net production rates were calculated as milligrams C fixed/gram dry weight/hour; the dry weight for *C. officinalis* included the skeletal CaCO₃. The methods concerning the handling of algae, incubation, and oxygen analysis were similar to those given by Littler and Murray (1974); however, the bottle size was increased to 1,220 ml and air-driven stirrers were used to circulate the water during incubation. Whole thalli were used in the experiments except in the case of *E. menziesii*, where ~5-cm-long segments of fronds were incubated.

3. *Calorific hypothesis.*—Calorific values should be comparatively lower in

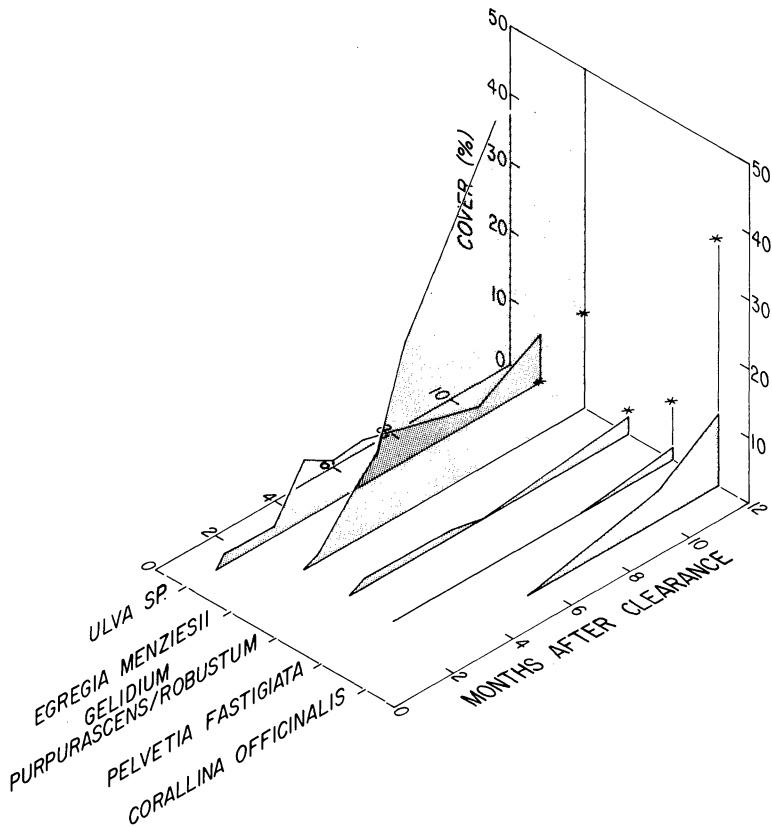


FIG. 1.—Twelve mo successional patterns of the five macrophytes chosen for study. Asterisks indicate the initial cover (%) levels of each species in the mature climax communities prior to clearance. (These data represent a portion of the results obtained by Murray and Littler [1978, in press]).

persistent climax algal species if selection has acted to increase structure at the cost of lipids and protoplasm in environmentally predictable habitats.

Samples of all five macroalgae were collected in December, 1974, and returned live to the laboratory where they were quickly cleaned in distilled water to remove salts, detritus, and epibiota. The algae were then dried at 80° C, ground to a fine powder in a ball mill, pelletized, and ignited in a Parr Model 1411 semimicro oxygen bomb calorimeter. An endothermy correction (Paine 1966) was applied to the samples of *C. officinalis* because of its high CaCO₃ component. The calorific content was expressed as kilocalories per ash-free gram dry weight after correcting for the percentage of ash, determined on single aliquots of the homogeneous milled samples (dried at 80° C) by igniting the material at 400° C for 24 h in a muffle furnace. Three replicates were run for each calorific determination.

4. *Predation hypothesis.*—Climax algae should be relatively resistant to grazing by generalist herbivores if selection has favored the evolution of antipredator defenses (e.g., toughness, low palatability, toxicity) in environmentally constant

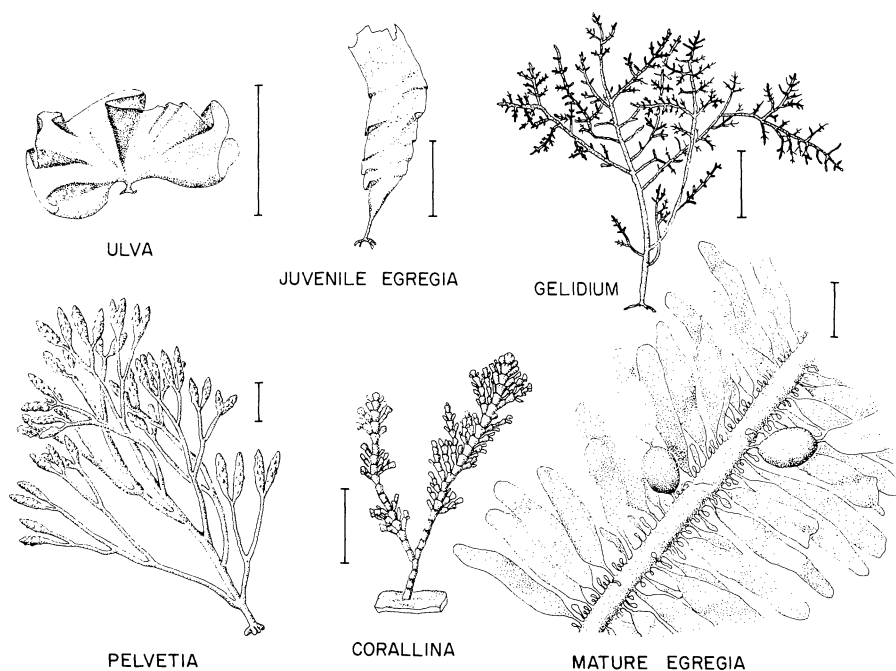


FIG. 2.—Thallus forms and sizes of representative specimens of the five experimental macrophytes. Scales represent 2.0 cm in each case; the portion of mature *Egregia* illustrated is from a thallus ~4 m long.

communities. *Strongylocentrotus purpuratus*, a generalist herbivore (Vadas 1977), was used to assess the palatability of the five experimental macroalgae. Experiments were run during March and May, 1978, in three 49×55 cm sections of a 540 liter refrigerated aquarium maintained at 17° – 20° C in the dark. During each experiment 20 urchins, fed on *Macrocystis pyrifera* prior to the experiment, were placed together in two of the three sections. The algae were collected from Laguna Beach, California, while submerged and returned immediately to the laboratory where they were separated into clumps of equal area (3×4 cm). Care was taken to ensure that the algae were not desiccated or mechanically injured in any way during handling.

The five algal species, on a grid (37×47 cm) containing 7 clumps per species (35 sample replicates) arranged in mechanically randomized patterns, were presented to the 20 urchins in each of the two chambers. Thirty-five similar samples were placed in the third section of the aquarium as controls to test for any loss of weight other than by grazing. The grids of algae were placed on the bottom of the aquarium for 48 h, whereupon the urchins immediately moved from the top of the aquarium to the bottom and began feeding. The total blotted wet weight of each replicate was measured before and after the grazing period.

5. *Structural hypothesis*.—Selection in environmentally constant habitats has tended to increase allocation of materials to nonpigmented supportive structure at the expense of photosynthetic tissue.

Cross sections approximately one cell thick were made by freezing microtome sectioning for all living thallus parts of the test algae, except for *Ulva* sp., which was examined directly. For each species, 10 different specimens were used. *Corallina officinalis*, because of its calcified nature, was not amenable to sectioning, so the percentage of skeletal CaCO_3 (81.7%) was determined and used as the value for nonphotosynthetic structure. For the other four experimental macroalgae, the percent pigmented and nonpigmented areas were calculated from fresh whole cross sections by means of a point intercept ocular grid and a Wild M20 fluorescence microscope which precisely revealed the location of pigmented plastids. Transects across each section were scored with a minimum replicated sample size (number of "hits") of > 100 .

6. *Wave-shearing hypothesis*.—Late successional species of macroalgae (if selected for persistence over long periods) should show a greater resistance to wave-shearing forces than opportunistic species (if selected primarily for rapid growth).

All five test algae were clamped between rubber-lined acrylic plates near their holdfasts and the plates bolted to the siltstone substratum at MLLW in the surf zone at Aliso Beach, California. The photographic technique (Littler 1980) was used to calculate the projected surface area of the 14–18 replicate algal fronds per species before and after exposure to surf for 24 h.

7. *Toughness hypothesis*.—Late successional macroalgae should possess tougher thalli than opportunistic algae if selection for structural tissue has occurred in temporally persistent species from mature communities.

A penetrometer similar to that of Feeny (1970) was used to measure frond "toughness" of the five macroalgae as follows. The middle portions of algal fronds were clamped between two rubber-lined acrylic plates across 8.0 mm-diameter holes that were carefully aligned on both plates. Several fronds, tightly arranged side by side, were used for *Corallina* and *Gelidium*. A plunger 7.8 mm in diameter, attached below a cup of weights, was carefully placed vertically through the hole in the top plate until it was supported by the algal thallus. Weights were then gently added until the plunger sheared through the thallus, at which time the total weight was recorded. Different specimens were used for each determination and 50 replicates were run for every species.

8. *Shifting-strategy hypothesis*.—During maturation, some macroalgae have the capacity to shift from an opportunistic strategy to one characteristic of late successional forms.

The time of appearance of juvenile and differentiated mature populations of *E. menziesii* in the successional experiments were contrasted. Additionally, six entire sheetlike juvenile individuals of *E. menziesii* were incubated during February, 1978 (under 15.0°C and ~ 70 klx), to compare with the production rates obtained for 5-cm portions of mature thalli (fig. 2) measured at the same time. The toughness of the juvenile sheetlike form of *E. menziesii* was similarly determined to compare with that of structurally differentiated individuals.

Data analysis.—The experimental design involved ranking the five test macroalgae on the basis of the six empirical features examined above. The significance ($P = .05$) of the means was assessed by single factor analysis of variance and the

Newman-Keuls multiple range test (Sokal and Rohlf 1969). Because the five experimental algae represent a range (continuum) of seral stages, one would not expect each mean to be statistically different from every other mean for a given parameter. However, species at opposite ends of the thallus-form spectrum (e.g., *Ulva* sp. and *Corallina officinalis*) should consistently show significant differences.

RESULTS

Successional studies.—Lateral vegetative encroachment by attached algae onto the newly cleared (disturbed) substrata was slight, and nearly all recruitment occurred from suspended reproductive bodies. Both the Santa Catalina and San Clemente Island successional study sites are dominated by macrophyte stocks, and recruitment during the studies consisted almost entirely of algae. During the first 0.8 mo following clearing, the experimental plots on San Clemente Island were repopulated mainly by microscopic species (e.g., Ectocarpaceae, colonial diatoms, and blue-green algae). At 1.3 mo, thin sheetlike forms, such as *Petalonia fascia*, *Scytosiphon lomentaria* (hollow sheet), and *Ulva* sp. (fig. 1)—were abundantly present along with the saccate cushion form *Colpomenia sinuosa*. Young sheet-like sporophytes of *Egregia menziesii* had appeared after 3.0 mo followed by *Pterocladia capillacea* (5.0 mo), and *Corallina officinalis* along with *Lithothrix aspergillum* at 6.0 mo. *Egregia menziesii* reached its maximum (106.0%—due to canopy overlap) 10.0 mo after clearance and *U. californica* (8.5%) at 4.0 mo.

Photosynthetic studies.—Figure 3 clearly indicates the ranking from high to low producers as follows: *Ulva* sp. (3.78 mg C fixed/g dry wt/h), *G. purpurascens/robustum* (1.36), *E. menziesii* (1.23), *Pelvetia fastigiata* (0.42), and *Corallina officinalis* (0.18). Only *G. purpurascens/robustum* and *E. menziesii* did not show significantly different net primary production rates ($P > .05$). Neither the productivity nor the maintenance costs hypotheses are falsifiable by these data (fig. 3); both are, in fact, strongly supported.

Calorific studies.—The calorific values for the experimental species, from highest to lowest (fig. 3) were *Ulva* sp. (5.44 kcal per ash-free g dry wt), *G. purpurascens/robustum* (4.62), *Pelvetia fastigiata* (4.17), *E. menziesii* (4.10), and *Corallina officinalis* (3.86). Each of the means was significantly different ($P < .05$) from all other means except those for *Egregia*, *Pelvetia*, and *Corallina*. The calorific hypothesis is generally supported except that *Pelvetia fastigiata* ranked somewhat higher in calorific content than predicted.

Predation studies.—The data (fig. 3) for percent thallus loss to urchin grazing over a 48 h period generally support the predation hypothesis, although none of the value pairs was statistically different ($P > .05$). We obtained a great deal of variability in our data (fig. 3) due to the fact that those test algae which were located early by urchins were more completely consumed than the replicate clumps found late in the experiment. Thus, we did not expect to obtain normally distributed data and, consequently, our 95% confidence intervals ranged from $\pm 38\%$ to $\pm 61\%$ of the means. The early successional alga *Ulva* sp. lost 43.1% followed by *Pelvetia fastigiata* (36.2%), *G. purpurascens/robustum* (22.9%), *E.*

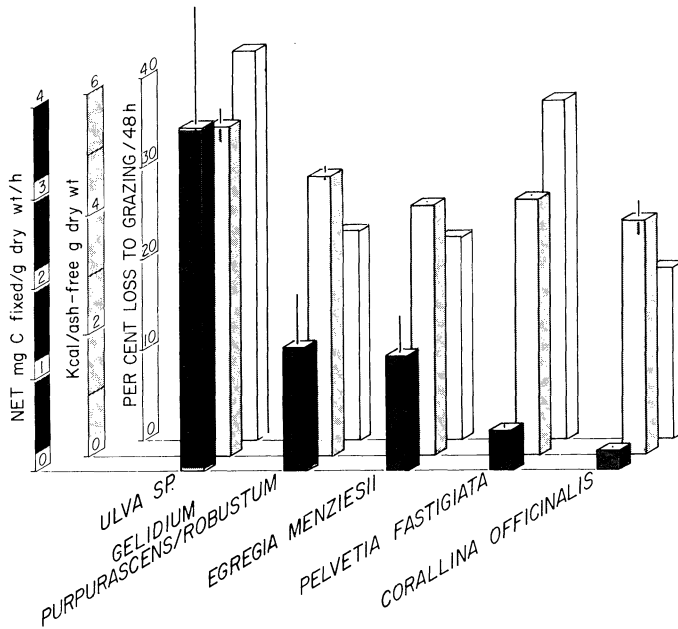


FIG. 3.—Mean net primary productivities (dark histograms in front), calorific values (medium histograms), and palatabilities (light histograms in rear) for the five experimental macrophytes. Confidence intervals (CI) of $\pm 95\%$ are given by straight lines at the top of each histogram; 95% CI for preferential feeding data ranged from $\pm 38\%$ to $\pm 61\%$ of means.

menziesii (22.6%), and the late seral species *Corallina officinalis* (19.6%). Only the climax species *Pelvetia fastigiata*, which occurs high in the intertidal (normally far removed from urchin predation), did not follow the prediction (table 1).

Structural studies.—*Ulva* sp. contained the lowest percentage of nonpigmented components (0.6%) in contrast to *G. purpurascens/robustum* (46.2%), *Pelvetia fastigiata* (57.3%), *Corallina officinalis* (81.7% CaCO_3), and *E. menziesii* (82.9%). Each of the means was significantly different ($P < .05$) from all other means. These data (fig. 4) strongly support the structural hypothesis.

Wave-shearing studies.—Based on the mean percentage of thallus loss due to wave shearing, the test species ranked as follows (fig. 4): *Ulva* sp. (95.6%), *Corallina officinalis* (28.2%), *Pelvetia fastigiata* (27.3%), *G. purpurascens/robustum* (14.3%), and *E. menziesii* (4.5%). *Ulva* sp. was significantly different ($P < .05$) from all other species and *Egrecia* was significantly different from *Corallina* and *Pelvetia*. This sequence generally supports the wave-shearing hypothesis, except for the articulated species *Corallina officinalis* which, because of its calcified brittle nature, was not amenable to clamping in the test apparatus by its flexible joints or without breaking its segments. No doubt this contributed to its lack of resistance to shearing as measured here and should not be interpreted as falsifying the hypothesis, especially in view of the personal observation that *Corallina* forms dense stands on vertical rock surfaces exposed to the most direct surf conditions in Southern California.

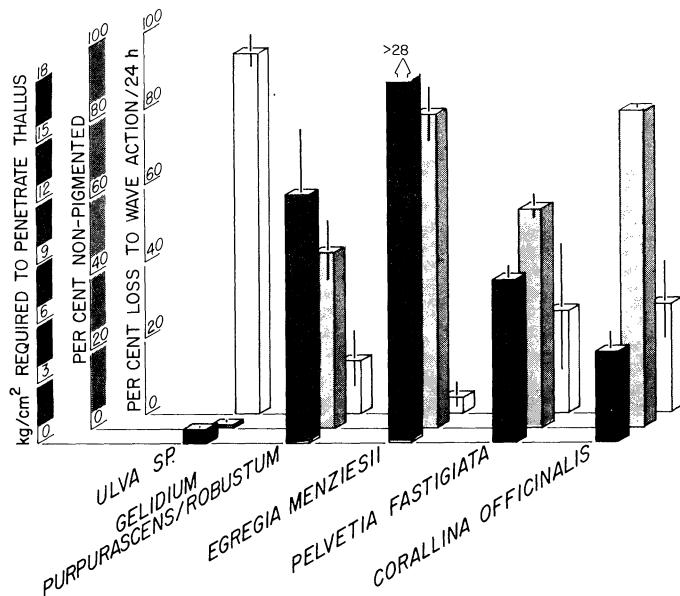


FIG. 4.—Frond toughness (dark histograms in front), percent structural components (medium histograms), and resistance to wave shock (light histograms in rear); \pm 95% CI are given by the straight lines at the top of each histogram.

Frond toughness studies.—*Egregia menziesii* (fig. 4) had the toughest thalli (> 28 kg/cm² to penetrate thallus) compared with *G. purpurascens/robustum* (12.4 kg/cm²), *Pelvetia fastigiata* (8.0 kg/cm²), *Corallina officinalis* (4.8 kg/cm²), and *Ulva* sp. (0.6 kg/cm²), thus generally supporting the toughness hypothesis. Single factor analysis of variance and Neuman-Keuls multiple range tests showed all means to be significantly different ($P < .05$). Again, *Corallina officinalis* was difficult to measure by this method due to its brittle nature, and results should not be regarded as contrary to the model (tables 1 and 2).

Shifting-strategy studies.—The juvenile (undifferentiated) sheetlike thalli of *E. menziesii* produced (table 3) at a rate nearly double that of the mature, structurally complex individuals, whereas the toughness of juvenile thalli was less than 13% that of the larger differentiated forms. These data, in conjunction with the observation that the juvenile blades (fig. 2) appeared quite early in succession (3.0 mo vs. 10.0 mo for fully differentiated thalli), as well as the fact that the large, highly structured mature fronds predominate (Littler and Murray 1975) in late successional communities, support the shifting-strategy hypothesis.

DISCUSSION

Algal succession has been interpreted long ago from the perspective of thallus-form groups (see Bokenham and Stephenson 1938; Northcraft 1948; and Fahey and Doty 1949). Neushul (1972) has been among the few to take a functional viewpoint by observing kelp community morphology in the field and relating it to

TABLE 3

COMPARATIVE VALUES FOR JUVENILE AND MATURE INDIVIDUALS OF *Egregia menziesii*
USED TO TEST THE SHIFTING-STRATEGY HYPOTHESIS

Thallus Used	Net Productivity (mg C fixed/g dry wt/h)	Toughness (kg/cm ² to penetrate thallus)	Time of Appearance on Successional Plots (mo)
Juvenile	2.51 ± .13	3.60 ± .33	3.0
Mature	1.26 ± .52	>28 (off scale)	10.0

water motion as an important selective factor. In addition, the biomechanical features (tensile strength and extensibility) of the kelp *Nereocystis luetkeana* have been examined (Koehl and Wainwright 1977) from a hydrodynamics perspective. Katada and Satomi (1975) also focused on the concept that the algae have evolved external forms and internal metabolic functions which enable them to persist under particular environmental conditions. These workers made the point that the "life-form" composition (i.e., incorporation of life history phenomena) of an algal community can be used to characterize the prevalent environmental conditions of a given habitat.

The thin sheetlike thallus form, represented in this investigation by *Ulva*, often has been noted (Bokenham and Stephenson 1938; Northcraft 1948; Fahey 1953; Littler and Murray 1975) as one of the very early colonizers of disturbed rocky-intertidal substrata. In the studies of Wilson (1925) and Murray and Littler (1978), other thin forms (i.e., *Scytosiphon lomentaria* and *Petalonia fascia*) grew rapidly to dominate the pioneer community and then disappeared, leaving crustose algal forms and juvenile thalli of long-lived macroalgae. Young, sheetlike juvenile sporophytes of *Egregia menziesii* appeared after only 3.0 mo and were abundant within 6.0 mo following the provision of new substratum (fig. 1); by the end of 10.0 mo *Egregia* had produced a spatially complex overstory of fully differentiated mature thalli. Although *Egregia menziesii* has been characterized (Littler and Murray 1975) as a *K*-selected long-lived dominant of mature intertidal communities, its juvenile sheetlike sporophytes are able to recruit effectively during early succession (fig. 1); also, production rates of juvenile *Egregia menziesii* (table 3) compare favorably with opportunistic forms such as *Ulva* (fig. 3).

Connell's (1975) successional model predicts that patches disturbed within relatively constant environments containing mature communities (e.g., the Santa Catalina and San Clemente Island study sites) will be colonized first by species having long reproductive seasons and producing large numbers of reproductive bodies. Littler and Murray (1975) extended the characteristics of this opportunistic (ephemeral) group to include macroalgae with rapid growth rates, high productivity, and simple thalli with large surface to volume ratios (see also Littler 1979). Similar studies of rocky-intertidal community development (e.g., Wilson 1925; Bokenham and Stephenson 1938; Northcraft 1948; Fahey 1953; Katada and Satomi 1975) have shown other early colonizers to be species with these same attributes.

It would appear from the productivity data (fig. 3) that selection has favored thin opportunistic species having high net productivity (and presumably rapid growth) in disturbed environments, while those thicker conspicuous species able to persist in less stressful, predictable habitats do so at the cost of lower photosynthetic rates and slower growth; this is due to their allocation of energy and materials to structural components that are not available for growth and reproduction (see tables 1 and 2). Littler (1979), also in partial support of the productivity and maintenance-costs hypotheses, found that 45 species of macroalgae, in thallus-form groups from highest to lowest producer on a dry weight basis, ranked as follows: thin sheetlike forms, finely branched forms, coarsely branched forms, thick forms, and prostrate epilithic forms. Odum et al. (1958), Kanwisher (1966), and King and Schramm (1976) likewise noted that finely branched forms showed higher production rates than coarsely branched species. A thallus-form more suited to obtaining light energy and nutrients would seem, as a working hypothesis, to explain the differences measured. Littler (1979) noted that the opportunistic species *Ulva californica*, *Enteromorpha* sp., and *Porphyra perforata* comprised a group with considerably higher net production rates than the other 42 algae measured. The extremely thin construction of these three minimizes internal self-shading; also, they have larger cells than most macroalgae, which results in relatively little self-shading by nonphotosynthetic wall components. Furthermore, since the thallus-form/productivity relationship was applicable (Littler 1979) over a broad latitudinal range including different habitats, it would appear that selection pressure for small thallus forms with rapid growth and high reproductive output (*r*-selection *sensu* Pianka 1970) as well as selection for large morphological forms having resistance to predation or to interference competition (*K*-selection) are widespread evolutionary forces among the macroalgae.

Grime (1977) proposed a three-part system of evolutionary strategies for terrestrial primary producers. These were (1) an opportunistic (ruderal), (2) a competitive, and (3) a stress-tolerant strategy, with the last cited by Grime (1977) as approximating the extreme "K-end" of the *r*- and *K*-selection continuum described by Pianka (1970). For aquatic macrophytes, the blue-green algae (Cyanophyta) and species of such genera as *Ulva*, *Enteromorpha*, and *Porphyra* are widely recognized as among the most stress resistant; however, in marked contrast to the examples for terrestrial plants (Grime 1977), these algae are capable of rapid growth and high reproductive output, thus placing them closer to the "*r*-end" of the continuum.

Calorific measurements (fig. 3) showed that climax species (e.g., *Corallina officinalis*) tended to be lower in calories than pioneer species (e.g., *Ulva* sp.), indicating that selection may have resulted in reduced nutritive value in algae characteristic of predictable environments (which are frequently exposed to predation owing to their spatially and temporally constant availability). Littler and Murray (1978) examined the calorific contents of 35 species of marine intertidal macroalgae and found that, in general, sheetlike forms with high surface to volume ratios (e.g., *Ulva californica*, *Pachydictyon coreaceum*, *Dictyota flabellata*) contained more energy than those with low ratios (e.g., *Ralfsia* sp., *Gigartina canaliculata*) or those with calcareous structure (e.g., *Corallina officinalis*, *Lithothrix aspergillum*). The projected surface area to volume ratios for the five

experimental algae used in the present study also corresponded to the calorific ranking pattern, with a high of $34.7 \text{ cm}^2/\text{cm}^3$ for *Ulva* sp. followed by *Corallina officinalis* (23.5), *Gelidium purpurascens/robustum* (20.7), *Pelvetia fastigiata* (12.7), and 7.9 for *Egregia menziesii* (see fig. 3 for calorific data). In agreement with the calorific hypothesis, Paine and Vadas (1969) emphasized that ranking for algal calorific values correlated with ranking for thallus longevity (i.e., ephemeral > annual > perennial). Littler and Murray (1978) also substantiated this finding but interpreted the relationship more directly in terms of morphological form. Macroalgae, such as *C. officinalis*, that contain a high ratio of structural to photosynthetic tissues (presumably of selective advantage in interference competition for space and light or protection from predation or physical stress [table 2]) have relatively less energy to allocate toward rapid growth and reproduction and tend to produce thalli with lower total calories per unit weight. In contrast, structurally simple opportunistic macroalgae that possess high production and growth rates with associated large surface to volume ratios (see Odum et al. 1958; Littler and Murray 1974; Littler, 1979) tend to have higher calorific content (fig. 3). The former typically are perennials characteristic of mature communities while the latter are usually ephemerals or annuals, and hence convey less temporal or spatial predictability to herbivores (Paine and Vadas 1969). Littler and Murray (1978) reported low calorific values for epilithic encrusting forms (e.g., *Hydrolithon decipiens*, *Pseudolithoderma nigra*, *Ralfsia* sp.). This observation verifies the suggestion (Paine and Vadas 1969) that encrusting forms, which are easily accessible, may have reduced their appeal to predators through evolution of thallus components that are low in nutritive content. The low values for articulated coralline algae (e.g., *C. officinalis*, *Haliptylon gracile*, *Lithothrix aspergillum*) obtained by Littler and Murray (1978) support the interpretation of Larkum et al. (1967) and Paine and Vadas (1969) that calcification and low calorific content may be important for survival under conditions of high grazing pressure by decreasing the energetic yield to the predator. Littler (1976) hypothesized five possible adaptive features of skeletal carbonate in marine algae, all of which are related to the model presented here (tables 1 and 2). An additional adaptive advantage may involve the ability of calcareous algae to modify their habitat; i.e., by providing their own optimal substrata, coralline algae (and green algae such as *Halimeda*) may themselves enhance the quality and environmental constancy of their microhabitats. It has been experimentally documented (Littler and Doty 1975) that the heavily calcified tropical alga *Porolithon onkodes* is physiologically adapted to withstand intense illumination and physically able to endure severe wave shock and grazing. It requires continuous disturbance, which prevents its competitive exclusion by frondose algae and corals.

Recently Vadas (1977), in his extensive study of feeding strategies in three different species of *Strongylocentrotus*, has clearly shown several causes for broad variations in urchin diets. The present preferential feeding information (fig. 3), although much more limited in scope than that of Vadas (1977), does suggest a trend supportive of the predation hypothesis. Opportunistic macrophytes such as *Ulva* would appear to be relatively susceptible to predation by generalist herbivores (fig. 3) compared with climax species, particularly the calcareous macroalga

C. officinalis. This finding agrees well with research (Lubchenco 1978) on the generalist snail *Littorina littorea* which primarily preferred small, tender ephemeral algae (such as *Ulva*, *Petalonia*, and *Scytosiphon*) that were cited as apparently lacking either structural or chemical means of deterring herbivores. Lubchenco (1978) similarly found that algal thalli in the lowest food preference category (e.g., *Ralfsia*, *Ascophyllum*) were all tough compared to those in the high category.

There appear to be two opposing forces influencing opportunistic species characteristic of pioneer macroalgal communities. The deployment of resources to rapid growth and high reproductive output not restricted seasonally could lead to a high degree of palatability (e.g., higher calorific value, fig. 3; less toughness, fig. 4); however, the temporal and spatial patchiness of newly cleared space for colonization in an intermediate or climax community would be expected to provide considerable refuge for early seral species. In environmentally constant habitats the patchiness and scarcity of opportunistic macroalgae may preclude any advantage to be gained by a given herbivore through specialization on such species. In contrast, conspicuous macrophytes characteristic of mature communities with their structural (and no doubt chemical) defenses should have reduced palatability (e.g., lower calorific values, fig. 3; increased toughness, fig. 4). Thus, the array of antiherbivore adaptations characteristic of later seral organisms may act to reduce the grazing ability of generalists and, because of genetic constraints, lead to increased specialization (divergent evolution). Correspondingly, Leighton (1969) showed a high degree of specialization on late successional subtidal macroalgae by various macroinvertebrates. This is somewhat at variance with models proposed (Ehrlich and Raven 1964; Rhoades and Cates 1976) for terrestrial plants; however, highly mobile grazers are not as prevalent in marine systems (except in tropical waters) and may not be as important as selective agents. Palatability determinations are extremely complex (cf. Cates and Orians 1975 and Otte 1975) and there are many biochemical considerations (e.g., 0.44 N H₂SO₄ in *Desmarestia* [Eppley and Bovell 1958]; halogenated compounds in certain Rhodophyta [Fenical 1975], diterpenoids and protein complexing tannins in Phaeophyta [McEnroe et al. 1977; Sieburth 1968; Ragan 1976]), in addition to the types of structural features dealt with here. For example, Odum (1969) pointed out the correlation between utilization of chemical defenses and the successional status of primary producers and Sieburth (1968) provided evidence that numerous algal compounds may be involved in allelopathy, increase resistance to pathogens, or act as deterrents to epiphytic (fouling) organisms. Also, a strategy possibly employed by highly productive opportunistic algae such as *Ulva* (table 1) might involve the rapid replacement of vegetative and reproductive tissues while at the same time satiating the appetites of predators. Such mechanisms have been proposed (Eckardt 1974; Dyer and Bokhari 1976) for terrestrial primary producers.

In terms of resistance to physical stress, the data (fig. 4), with the exception of *C. officinalis* (noted earlier as artifactual), indicate that intermediate and climax algae have gained persistence in time at the cost of decreased growth rates and reproductive output by allocating significant quantities of energy and materials to

structural components. All of the experiments involving resistance to shearing, frond toughness, and the results on the percent nonphotosynthetic versus photosynthetic tissue (fig. 4) strongly substantiate this viewpoint (hypotheses 5, 6, and 7). A relevant point which has appeared in the literature (Dayton 1975) concerns the physical capacity of tough algae such as *Lessoniopsis* to remove nearby organisms such as *Hedophyllum* by a wave-induced whiplash effect.

The ability of *Egregia menziesii* for early recruitment (fig. 1) and the thin sheet-like nature and high productivity of its young, undifferentiated individuals compared to older, highly structured thalli (table 3, fig. 2) indicate a shift in thallus-form strategies (hypothesis 8). This allows *Egregia menziesii* (and presumably most of the other Laminariales) to compete effectively for newly cleared space with opportunistic forms as well as to persist among late successional competitors for light and space.

Also, we mentioned earlier that the life histories of many species of algae include two to several alternate thallus forms. For example, it is probable from the data presented here that the sheetlike phase of *Petalonia fascia* or the complanate form of *Scytosiphon lomentaria* (Clayton 1976) have evolved through adaptations to selective forces that favor opportunism. In contrast, their *Ralfsia*-like epilithic crustose phases (Wynne 1969; Clayton 1976) may have evolved under markedly different selective pressures, such as intense grazing, stressful winter conditions, or sand scouring. The encrusting alternate of *Gigartina papillata*, *Petrocelis middendorffii* (West 1972) has been shown to grow very slowly, to have low recruitment and mortality rates, and to be capable of persisting to great age (Paine et al. 1979). The co-occurrence of such heteromorphic stages of the same organism (e.g., *Scytosiphon*, *Petalonia*, and their ralfsioid forms) which were found simultaneously by Murray and Littler (1978) suggests that some algae are able to "hedge their bets" against local extinction by concurrently adopting strategies at both ends of the spectrum presented in tables 1 and 2. Further support of this "heteromorphic life histories hypothesis" is provided by contrasting the upright blade form of *Gigartina papillata* with its long-lived crustose alternate, *Petrocelis middendorffii*. The former is significantly ($P < .05$) more productive (0.64 vs. 0.09 mg C fixed/g dry wt/h) and 2.5 times more palatable (significant at $P < .05$, Mann-Whitney *U*-test) than the latter using the methods presented earlier.

Life-form classification schemes have been proposed by many phycologists (e.g., Funk 1927; Feldmann 1938, 1951, 1966; Katada and Satomi 1975; Chapman and Chapman 1976); however, none of these have proven to be entirely satisfactory. The primary reason is that they have been restricted to external morphological features (i.e., thallus form *sensu* Funk 1927), a combination of morphological and life-history attributes (i.e., life form *sensu* Katada and Satomi 1975), or both of these in conjunction with general habitat information (Chapman and Chapman 1976). We believe a major shortcoming has been the failure to examine ecological interactions and physiological aspects (i.e., functional form as presented here) which must be considered before a realistic and truly utilitarian interpretation of "forms" in the algae can be forthcoming.

The present study has attempted to develop a synthetic "functional form" paradigm concerning important adaptive correlates of algal structure relative to

biological function and, by means of a costs versus benefits analysis, to begin to test several of the predictions inherent in the model. In developing a theory dealing with form and function from a strategic perspective, it has been necessary to pose many questions while answering relatively few. However, it is anticipated that this approach will stimulate new insights concerning algal morphology and natural history viewed from a functional perspective.

SUMMARY

A synthetic "functional form" paradigm concerning hypothetically important adaptive features of algal structure and function was developed and tested by a costs/benefits strategic approach. Successional manipulations were performed by disturbing mature, environmentally constant intertidal communities; from the array of colonizing macroalgae, *Ulva* sp. was chosen as an opportunistic representative of pioneer seral stages, *Egrecia menziesii* and *Gelidium purpurascens/robustum* as intermediate to late seral species, and *Pelvetia fastigiata* and *Corallina officinalis* as characteristic of more mature climax communities. The ranking from high to low primary producers (*Ulva* > *Gelidium* > *Egrecia* > *Pelvetia* > *Corallina*) indicates that selection in fluctuating environments has favored opportunistic species having high net productivity, while those species able to persist in benign predictable habitats do so at the cost of lower photosynthetic rates and presumably slower growth. The kilocalories per ash-free gram dry weight from highest to lowest species were *Ulva* (5.44), *Gelidium* (4.62), *Pelvetia* (4.17), *Egrecia* (4.10), and *Corallina* (3.86). With the exception of *Pelvetia*, which occurs high in the intertidal, these calorific values suggest that selection has tended to reduce nutritive content in climax algal forms. The results for percent thallus loss to urchin grazing over a 48 h period generally support the hypothesis that selection has differentially favored the evolution of antipredator defenses in environmentally constant macrophyte communities; *Ulva* lost considerably more of its blotted wet weight (43.1%) compared to *Pelvetia* (36.2%), *Gelidium* (22.9%), *Egrecia* (22.6%), and the late seral form *Corallina* (19.6%). *Ulva* contained the lowest percentage of nonpigmented (structural) components (0.6%), followed by *Gelidium* (46.2%), *Pelvetia* (57.3%), *Corallina* (81.7% CaCO₃), and *Egrecia* (82.9%) which indicates that selection in mature communities has tended to increase allocation of materials to nonpigmented supportive structure at the expense of photosynthetic tissue. Later successional macroalgae showed greater toughness as well as greater resistance to wave-shearing forces than the opportunistic species, thus implicating selection for persistence as opposed to rapid growth in climax communities. Data on succession, productivity, and toughness indicate that *E. menziesii* shifts from an opportunistic strategy during its juvenile stages to a highly differentiated complex form able to persist in mature successional stages. The co-occurrence of different morphological phases of the same species (e.g., *Scytosiphon lomentaria*, hollow sheet; *Petalonia fascia*, sheet; and their *Ralfsia*-like forms, crusts), along with information contrasting productivity, palatability, and longevity between *Gigartina papillata* and its crustose alternate *Petrocelis*

middendorffii, suggests that some algae have the capacity to concurrently adopt strategies of both opportunistic and climax algal forms.

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LITERATURE CITED

- Abbott, I. A., and G. J. Hollenberg. 1976. Marine algae of California. Stanford University Press, Stanford, Calif.
- Bokenham, N. A. H., and T. A. Stephenson. 1938. The colonization of denuded rock surfaces in the intertidal region of the Cape Peninsula. *Ann. Natal Mus.* 9:47-81.
- Cates, R. G., and G. H. Orians. 1975. Successional status and the palatability of plants to generalized herbivores. *Ecology* 56:410-418.
- Chapman, V. J., and D. J. Chapman. 1976. Life forms in the algae. *Bot. Mar.* 19:65-74.
- Clayton, M. N. 1976. The morphology, anatomy and life history of a complanate form of *Scytosiphon lomentaria* (Scytosiphonales, Phaeophyta) from southern Australia. *Mar. Biol.* 38:201-208.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460-490 in M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Belknap, Cambridge, Mass.
- Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45:137-159.
- Dyer, M. I., and U. G. Bokhari. 1976. Plant-animal interactions: studies on the effects of grasshopper grazing on blue gramma grass. *Ecology* 57:762-772.
- Eckardt, F. E. 1974. Life form, survival strategy and CO₂-exchange. Pages 57-59 in *Proceedings of the first international congress of ecology*. Centre for Agricultural Publishing and Documentation, Wageningen.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586-608.
- Eppley, R. W., and C. R. Bovell. 1958. Sulfuric acid in *Desmarestia*. *Biol. Bull.* 115:101-106.
- Fahey, E. M. 1953. The repopulation of intertidal transects. *Rhodora* 55:102-108.
- Fahey, E. M., and M. S. Doty. 1949. Pioneer colonization on intertidal transects. *Biol. Bull.* 97:238-239.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51:565-581.

- Feldmann, J. 1938. Recherches sur le végétation marine de la Méditerranée. La côte des Albères. Rev. Algol. 10:1-339.
- . 1951. Ecology of marine algae. Pages 313-334 in G. M. Smith, ed. Manual of phycology. Ronald, New York.
- . 1966. Les types biologiques d'algues marines benthiques. Mém. Soc. Bot. Fr. 1966:45-60.
- Fenical, W. H. 1975. Halogenation in the Rhodophyta: a review. J. Phycol. 11:245-259.
- Funk, G. 1927. Die Algenvegetation des Golfs von Neapel. Pubbl. Stn. Zool. Napoli Suppl. 7:1-507.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111:1169-1194.
- Kanwisher, J. W. 1966. Photosynthesis and respiration in some seaweeds. Pages 407-420 in H. Barnes, ed. Some contemporary studies in marine science. Allen & Unwin, London.
- Katada, M., and M. Satomi. 1975. Ecology of algae. Pages 211-239 in J. Tokida and H. Hirose, eds. Advance of phycology in Japan. Gustav Fischer Verlag, Jena.
- King, R. J., and W. Schramm. 1976. Photosynthetic rates of benthic marine algae in relation to light intensity and seasonal variations. Mar. Biol. 37:215-222.
- Koehl, M. A. R., and S. A. Wainwright. 1977. Mechanical adaptations of a giant kelp. Limnol. Oceanogr. 22:1067-1071.
- Larkum, A. W. D., E. A. Drew, and R. N. Crossett. 1967. The vertical distribution of attached marine algae in Malta. J. Ecol. 55:361-371.
- Leighton, D. L. 1966. Studies of food preference in algivorous invertebrates of southern California kelp beds. Pac. Sci. 20:104-113.
- Littler, M. M. 1976. Calcification and its role among the macroalgae. Micronesica 12:27-41.
- . 1979. Morphological form and photosynthetic performances of marine macroalgae: tests of a functional/form hypothesis. Bot. Mar. 22 (in press).
- . 1980. Overview of the rocky intertidal systems of southern California. In D. M. Power, ed. The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, Calif. (in press).
- Littler, M. M., and M. S. Doty. 1975. Ecological components structuring the seaward edges of tropical Pacific reefs: the distribution, communities and productivity of *Porolithon*. J. Ecol. 63:117-129.
- Littler, M. M., and S. N. Murray. 1974. The primary productivity of marine macrophytes from a rocky intertidal community. Mar. Biol. 27:131-135.
- . 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. Mar. Biol. 30:277-291.
- . 1978. Influence of domestic wastes on energetic pathways in rocky intertidal communities. J. Appl. Ecol. 15:583-595.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112:23-39.
- McEnroe, F. J., K. J. Robertson, and W. H. Fenical. 1977. Diterpenoid synthesis in brown seaweeds of the family Dictyotaceae. Pages 179-189 in D. J. Faulkner and W. H. Fenical, eds. Marine natural products chemistry. Plenum, New York.
- Mann, K. H. 1973. Seaweeds: their productivity and strategy for growth. Science 182:975-981.
- Murray, S. N., and M. M. Littler. 1978. Patterns of algal succession in a perturbed marine intertidal community. J. Phycol. 14:506-512.
- . (in press). Analysis of the patterns of recovery of intertidal and subtidal communities. Pages III-1.1.20-1-III-1.1.2-266 in M. M. Littler, ed. The annual and seasonal ecology of Southern California rocky intertidal, subtidal, and tidepool biotas. Southern California baseline study, year two, final report. Vol. III, Rep. 1.1. Bureau of Land Management, Department of the Interior, Washington, D.C.
- Neushul, M. 1972. Functional interpretation of benthic marine algal morphology. Pages 47-73 in I. A. Abbott and M. Kurogi, eds. Contributions to the systematics of benthic marine algae of the North Pacific. Japanese Society of Phycology, Kobe.
- Northcraft, R. D. 1948. Marine algal colonization on the Monterey Peninsula, California. Am. J. Bot. 35:396-404.
- Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262-270.

- Odum, E. P., E. J. Kuenzler, and M. X. Blunt. 1958. Uptake of P^{32} and primary productivity in marine benthic algae. *Limnol. Oceanogr.* 3:340–345.
- Otte, D. 1975. Plant preference and plant succession. *Oecologia* 18:129–144.
- Paine, R. T. 1966. Endothermy in bomb calorimetry. *Limnol. Oceanogr.* 11:126–129.
- Paine, R. T., C. J. Slocum, and D. O. Duggins. 1979. Growth and longevity in the crustose red alga *Petrocelis middendorffii*. *Mar. Biol.* 51:185–192.
- Paine, R. T., and R. L. Vadas. 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. *Mar. Biol.* 4:79–86.
- Pianka, E. R. 1970. On *r*- and *K*-selection. *Am. Nat.* 104:592–597.
- Ragan, M. A. 1976. Physodes and the phenolic compounds of brown algae. Composition and significance of physodes *in vivo*. *Bot. Mar.* 19:145–154.
- Rhoades, D. F., and R. G. Cates. 1976. Toward a general theory of plant antiherbivore chemistry. Pages 168–213 in J. W. Wallace and R. L. Mansell, eds. *Recent advances in phytochemistry*. Plenum, New York.
- Seigler, D. S. 1977. Primary roles for secondary compounds. *Biochem. Syst. Ecol.* 5:195–199.
- Seigler, D. S., and P. W. Price. 1976. Secondary compounds in plants: primary functions. *Am. Nat.* 110:101–105.
- Sieburth, J. M. 1968. The influence of algal antibiosis on the ecology of marine microorganisms. Pages 63–94 in M. R. Droop and E. J. Ferguson Wood, eds. *Advances in microbiology of the sea*. Academic Press, New York.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. Freeman, San Francisco.
- Vadas, R. L. 1977. Preferential feeding: an optimization strategy in sea urchins. *Ecol. Monogr.* 47:337–371.
- West, J. A. 1972. The life history of *Petrocelis franciscana*. *Br. Phycol. J.* 7:299–308.
- Wilson, O. T. 1925. Some experimental observations of marine algal successions. *Ecology* 6:303–311.
- Wynne, M. J. 1969. Life history and systematic studies of some Pacific North American Phaeophyceae (brown algae). *Univ. Calif. Publ. Bot.* 50:1–88.