Heterotrichy and Survival Strategies in the Red Alga *Corallina officinalis* L.

M. M. Littler and B. J. Kauker*

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

* *Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717, U.S.A.*

Abstract

The adaptive significance of heterotrichy was investigated for the abundant and widespread articulated coralline alga *Corallina officinalis* L., using a functional-form approach. The importance of the basal crust to the resiliency of this species was examined by physically disturbing mature, temporally-constant intertidal communities in southern California. Areas scraped to remnant crusts recovered four times more rapidly than did flame-sterilized plots. This regenerative capacity is advantageous to *C. officinalis* by permitting (1) retention of primary space during disturbances as well as (2) accelerated recovery to predisturbance abundances. Additionally, continued outward radiation and proliferation by the basal crust gives the alga considerable advantage over non-heterotrichous species in sequestering new space. The primary productivity relationship was as predicted (fronds = 0.19 mg C g dry wt^{-1} h^{-1}, crusts = 0.08). The crusts had significantly (P < 0.01) greater penetration toughness than the fronds (94 and 43 g mm^{-2} to penetrate, respectively) as well as being more resistant to sea urchin grazing (2% vs. 94% lost $\cdot$ 48 h^{-1}), in conformity with a previously published functional-form model. However, calorific values were low and not significantly different (P > 0.05) between the frondose and crustose portions (1.47 and 1.90 kcal $\cdot$ ash-free g dry wt^{-1}, respectively). It is probable that opposing selective forces have resulted in the divergence of specialized thallus morphologies and concomitant physiological responses in differentiated algae such as *C. officinalis*. The resultant products represent options that spread the risk from different sources of mortality. Also, because heterotrichy is so abundantly represented and of widespread ocurrence in rocky-intertidal and subtidal communities, the phenomenon warrents more attention than has been given by most marine ecologists.

Introduction

Evolution among marine macroalgae has resulted in an exotic array of morphologies, life-histories, physiological reactions, biochemical products and phenotypic plasticities. Such features comprise the basis for traditional marine algal systematics and have been used to describe new species or to speculate on phylogenetic affinities. While these approaches are valuable, a fresh outlook is needed to provide mechanistic evolutionary interpretations of morphological attributes.

Dixon (1965) was among the first to provide insight into the ecological significance of macroalgal heterotrichy and pointed out that perennation from recumbent thalli is critical to the longevity of some marine species with differentiated prostrate as well as upright portions. Heterotrichy was defined (Fritsch 1935, p. 20) to describe all cases where the algal thallus consists of two distinct parts: (1) a prostrate creeping system usually exhibiting apical growth and functioning as a holdfast, that gives rise to (2) an erect system which is usually branched. This definiti-

on is extended herein (see also Dixon 1973, p. 83) to include plant axes as well as filament types.

Neushul (1972) provided an early hypothesis concerning comparative hydrodynamic constraints on alternate heteromorphic stages of kelps (Laminariales). The term "heteromorphic" was originally used (Kylin 1938, Smith 1938) specifically to describe those members of the Phaeophyta having two dissimilar life-history phases and has been misused in the recent ecological literature to refer to the *Bonnemaisonia*-type life history found in the Rhodophyta (see Dixon 1973, p. 184). All Rhodophyta have dissimilar morphological stages due to the presence of a carposporophyte generation, hence, "heteromorphic" is uninformative in reference to red algal life histories. Among the first evolutionary suggestions (Vadas 1979) was that dissimilar algal life-history phases may have resulted from simultaneous bimodal selection pressures toward the extreme ends of an r-K continuum (see Pianka 1970).

Data confirming the adaptive importance of life histories with dissimilar morphological phases has been subsequently forthcoming. The greater resistance of crustose life-history stages to herbivory is clearly substantiated (Littler and Littler 1980, 1983, Lubchenco and Cubit 1980, Slocum 1980, Dethier 1981). Contrastingly, the upright stages tend to be relatively tender, more susceptible to grazers, higher in calorific value, more productive and contain greater proportions of photosynthetic vs. structural tissue (Littler and Littler 1983). During maturation, some macroalgae (e. g., kelps) functionally shift from an opportunistic strategy (*sensu* Grime 1979) to one characteristic of persistent late-successional forms (Littler and Littler 1980). However, the functional significance of heterotrichy (*sensu* Fritsch 1935) within an individual plant such as *Corallina officinalis* has not been tested experimentally and could represent a widespread and important survival strategy among the marine macroalgae.

In this paper, we will examine the general hypothesis that the evolutionary history of *Corallina officinalis* has led to a dichotomy of divergent metabolic, ecological and morphological adaptations within individual plants, by analyzing the basal crustose portion as well as the upright frondose thallus from the perspective of the functional-form model. The morphological differences should reflect quite different survival strategies (Littler and Littler 1980) in terms of trade-offs between capacities for rapid growth and productivity, reproduction, environmental tolerance, resistance to predation and competition (for nutrients, space and light). This prediction was directly assessed by measuring resilience to physical disturbance as well as morphological, physiological, calorific, predation-tolerance and physical qualities of the two forms during laboratory and field experiments.

Materials and Methods

The Alga

The heterotrichous alga *Corallina officinalis* L. (Corallinaceae, Rhodophyta; Fig. 1) was the organism chosen for study. This species, together with another articulated coralline, *C. vancouveriensis* Yendo, provides the major intertidal macrophytic cover (9% mean cover each) throughout the Southern California Bight (Littler 1980a), where it is also the most frequently encountered macrophyte (occurring in 46% of all samples). *Corallina officinalis* consists of a prostrate, crustose, sterile base that gives rise to multiple, upright, articulated, pinnately-branched fronds that contain the reproductive structures. The upright fronds are well known for their broad range of phenotypic plasticities (Setchell and Gardner
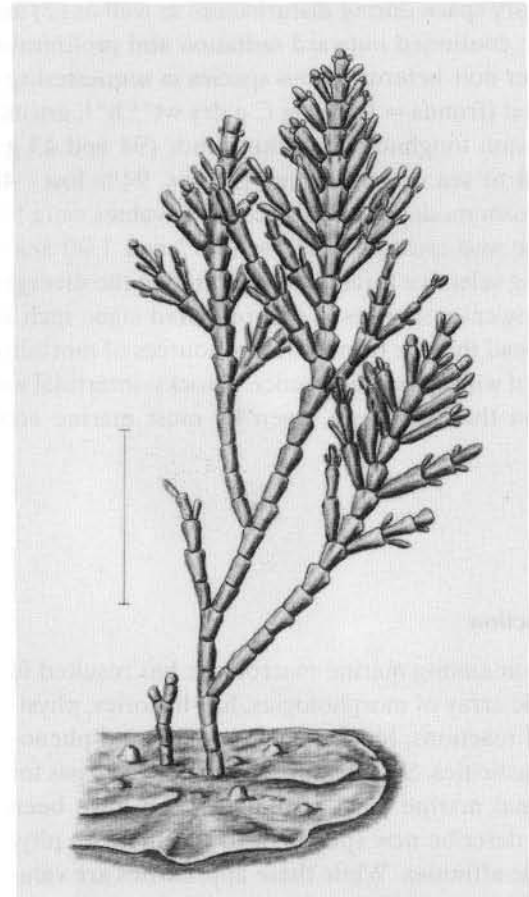

Fig. 1. Upright frondose and prostrate crustose portions of a representative specimen of *Corallina officinalis* from southern California (scale = 1.0 cm).

1903, Foslie 1905, Rosenvinge 1917, Johansen and Colthart 1975) and, for this reason, we chose not to recognize the epithet, var. *chilensis*, to which others often refer northeastern Pacific coast material. The plant is heavily calcified (~74% $CaCO_3$) and has vegetatively similar tetrasporangial and gametangial phases.

Study Area

San Clemente Island, the southernmost and fourth largest of the Southern California Islands, is located approximately 70 km seaward of Los Angeles Harbor and 113 km northwest from San Diego, California. As a consequence of its distance from the populous mainland and its strictly regulated access, the marine biota is among the most pristine in southern California (Littler and Murray 1975). The study site is located approximately 550 m to the south of the southern promontory delineating Wilson Cove (33° 00′ 06″ N, 118° 33′ 03″ W).

Resilience to Physical Disturbance

We re-investigated successional samples previously obtained by Murray and Littler (1978, 1979) for the identical study site and a summary of relevant methods is presented here. Eight 20 × 50 cm permanently-marked plots were photographed and then mechanically cleared of upright macroorganisms with the aid of scraping tools. The plots were located between +0.2 and +0.5 m relative to mean lower low water in an undisturbed community dominated by a continuous turf of *Corallina officinalis* and foliose overstory algae. The clearing procedures were effective in producing disturbed plots devoid of all macroorganisms except for some encrusting species and abundant basal thalli of *C. officinalis*. Additionally, four of these plots were scrubbed with wire brushes and sponges thoroughly soaked in 70% ethanol and then scorched for about one hour with portable propane torches. All eight plots were rephotographed with infra-red film which records the chlorophyll fluorescence of living plant material. The four torched plots were revealed to be completely sterilized, whereas the scraped plots contained extensive living basal crusts of *C. officinalis*. Subsequent recolonization and recovery of *C. officinalis* was monitored for the following 12 mo by the photogrammetric technique (Littler 1980a).

Productivity and Respiration

Measurements of net photosynthesis and respiration were made (six whole-portion replicates for each of the two thallus forms) during 3 May 1981 on San Clemente Island between 0900 and 1400 h at 16.0 °C under overcast skies of about 44 klx. Net productivity and respiration were calculated as milligrams C fixed g dry wt^{-1} h^{-1} from measurments of oxygen flux (assuming a P.Q. and R.Q. of 1.00). The methods involving handling, incubation and O_2 analysis were identical to those detailed by Littler (1980b). For the basal portions, rock fragments containing thalli were cleared of upright fronds, other plant materials and animals by careful use of forceps and a scalpel. Several control rocks without *C. officinalis* crusts were treated in this way and confirmed that the scraping was effective in eliminating measurable production or respiration when the scraped substrata alone were incubated. Dry weight was determined directly for the upright fronds and for the crustose bases after they were removed from the rock substrata prior to drying. The dried material was then ignited at 500 °C to constant weight in a muffle furnace and ash-free dry weight was calculated.

Predation Resistance

Strongylocentrotus purpuratus (Stimpson), a herbivore with a diverse diet (Vadas 1977, Littler and Littler 1980, Sousa *et al.* 1981), was used to assess the resistance to predation of the two algal forms. This sea urchin occurs in intertidal pools in southern California where it frequently (pers. obs.) encounters both of the forms examined. Experiments were run during 29—31 August 1981 in three 49 × 55 cm sections of a 540-liter refrigerated aquarium maintained at 17—20 °C under the natural light-dark regime (indirect light). During each experiment, 20 urchins, fed on *Macrocystis pyrifera* (L.) C. Ag. and then starved for one week prior to the experiment, were placed together in two of the three sections. The alga was collected while submerged and returned immediately to the laboratory where thalli were separated into preweighed clumps or rock fragments of equal, two-dimensional thallus area (3 × 4 cm). Care was taken to ensure that the specimens were not desiccated or unduly injured. However, it was necessary to clip off uprights from the basal portions, and crusts were presented on fragments of the natural rock substratum after retention for 24 h in running seawater to permit wound healing. The two algal forms, on a grid (37 × 47 cm) containing 12 clumps per form arranged in an alternating pattern, were presented to the 20 urchins in each of the two chambers. A third similar grid was placed in the remaining section of the aquarium to control for loss of weight other than by grazing. After 48 h on the bot-

tom of the aquarium, the blotted weight of each replicate was determined again on an analytical balance and used to ascertain the percent lost to grazing.

Penetration Resistance

A penetrometer identical to that of Littler and Littler (1983) was used to measure penetration resistance of the two freshly-collected thallus forms. The crustose thalli were carefully chipped from the underlying substratum with a thin palette knife, which proved to be quite difficult due to the brittleness of individual plants. The middle portions of fronds were gently clamped between two acrylic plates across 3.00 mm-diameter holes that were precisely aligned on both plates. A cylindrical steel plunger 2.98 mm in diameter with blunted edges, attached below a 0.5-liter plastic cup, was placed carefully through the hole in the upper plate so that it rested on the algal thallus. Metal washers were then gently placed into the cup until the plunger penetrated through the thallus, at which time the total weight of the device was measured and recorded. Different individuals were analysed for every determination and 25 replicates were run for each of the two forms.

Calories

Samples of both forms were collected on 1 July 1981 and returned to the laboratory where they were cleaned of epibiota and quickly dipped in distilled water to remove salts. The thalli were than dried to constant weight at 80 °C, ground to a fine powder in a ball mill, pelletized and ignited in a semimicro, oxygen bomb calorimeter (Parr Model 1411). The calorific content was expressed as kilocalories per ash-free gram dry weight after correcting for the percentage of ash. An endothermy conversion (Paine 1966) was applied because of the high $CaCO_3$ content. Six replicates were determined for each morphological form.

Results

Testable hypotheses were postulated by considering possible selective pressures on the crustose thallus portions of Corallina officinalis in contrast to those leading to the differentiated, more complex, upright fronds. From these non-mutually-exclusive considerations, the extremes of a broad range of functional features for the two forms could be examined as follows.

1. Disturbance Hypothesis

The crustose portion of C. officinalis should show greater resistance to physical damage than the upright thallus, if the former is adapted to increase resiliency of the alga following disturbance.

The data afford strong support of the disturbance hypothesis as follows. In the four sterilized plots (Fig. 2), upright articulated fronds of Corallina officinalis did not appear until 6.0 mo after the disturbance. Their cover increased steadily until the last month (month 12) of the study, at which time they covered an average of 10%. Contrastingly, the regenerated upright C. officinalis, in the other four plots scraped to basal remnants but not sterilized (Fig. 2), had exceeded this 12-mo value in only one fourth of the time (month 3) and reached nearly double the cover (18%) by the twelfth month. Herbivorous gastropods and sea urchins were never recorded in any of the disturbed quadrats, probably because the plots were located in the midst of an otherwise undisturbed algal-turf dominated zone. Additionally, lateral encroachment by organisms adjacent to the plots was minimal.
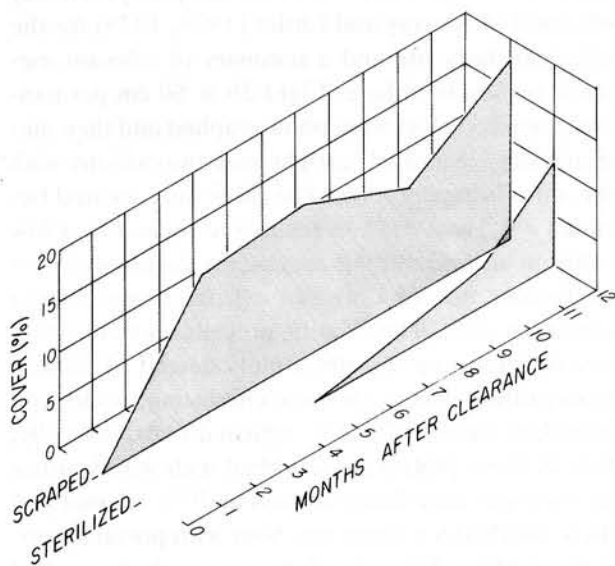

Fig. 2. Recovery of upright fronds following disturbance in flame-sterilized and scraped experimental plots (N= 4 per treatment).

2. Productivity Hypothesis

The upright frondose portion of C. officinalis should tend to show higher primary production rates than the crustose portion, if the former is better adapted to compete for light and nutrients.

In agreement with the productivity hypothesis, the six frondose specimens of Corallina officinalis (Fig. 3A) fixed 0.19 mg C g dry wt^{-1} h^{-1}, a value 2.4 times

that of the six epilithic crustose samples (0.08, significantly different at $P < 0.001$, ANOVA). Respiration rates were not statistically different ($P > 0.1$) between the six separate upright and six prostrate forms (0.07 and 0.04 mg C g dry $wt^{-1} h^{-1}$, respectively).

3. Predation Hypothesis

In conjunction with hypotheses 1 and 5, the crustose thalli of *C. officinalis* should have greater resistance to herbivory (physical damage) than the upright portions, if the crust represents an option that decreases mortality from predators.

The data for mean thallus losses to sea urchin grazing over a 48-h period (Fig. 3B) were: 24 crustose thalli = 2% lost and 24 frondose thalli = 94% lost (significantly different at $P < 0.001$), in strong support of the predation hypothesis.
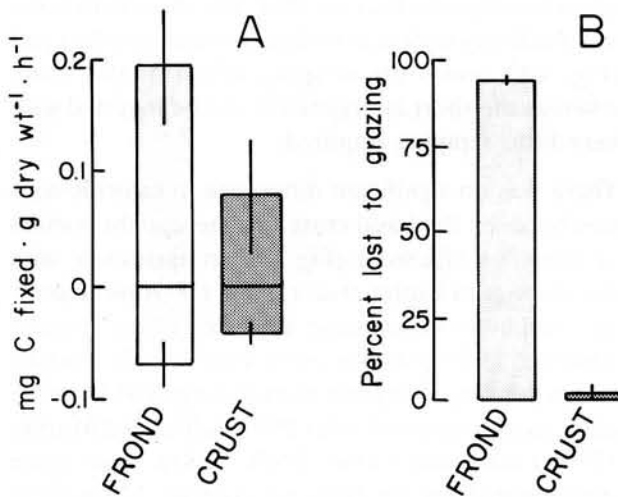

Fig. 3. A. Mean net primary productivity (N = 6) and respiration (N = 6) for the two portions. Lines indicate ±S.D. (standard deviation).
B. Susceptibility to sea urchin grazing per 48 h (N = 24).

4. Toughness Hypothesis

The two forms of *C. officinalis* should show a significant difference in toughness, with crusts being tougher than fronds, if directly related to thallus longevity and persistence.

The 25 crustose bases measured (Fig. 4A) had nearly double (significantly greater at $P < 0.01$, ANOVA) the penetration resistances (mean = 94 g mm^{-2} to penetrate thallus) of the 25 upright fronds (43 g), in agreement with the prediction.

5. Calorific Hypothesis

In association with hypothesis 3, calorific yields to predators should be lower in the crustose portions than in the upright fronds, since crusts are more readily accessible to the predominantly epilithic herbivores.

The mean calorific values (Fig. 4B) were 1.90 K cal · ashfree g dry wt^{-1} for the six crustose individuals measured and 1.47 for the six upright fronds. These values are not significantly different ($P > 0.05$), thereby falsifying the calorific hypothesis.
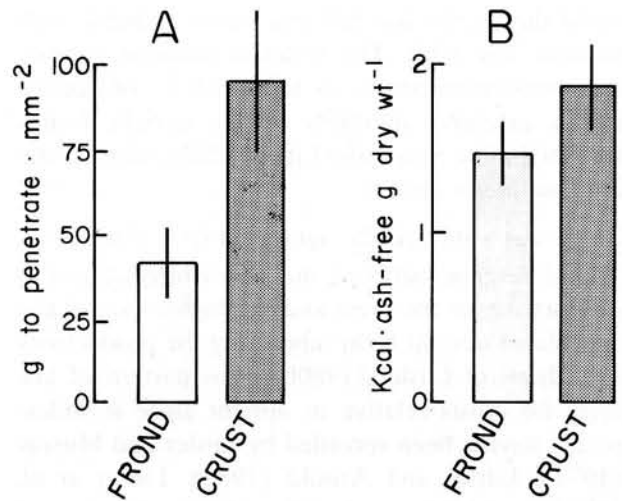

Fig. 4. A. Mean resistance to penetration ±S.D. (N = 25).
B. Ash-free free calorific values (N = 6).

Discussion

In the scraped plots, the remnant basal crusts of *Corallina officinalis* recovered rapidly from the mechanical disturbance (Fig. 2) and produced 14% cover of new upright fronds within three months. This vegetative regrowth reduced the time needed by *C. officinalis* to repopulate an equivalent sterile area by means of suspended reproductive bodies to one fourth (Fig. 2, sterilized plots). The ability to recover from resistant vegetative portions is advantageous to *C. officinalis* in that it allows (1) the retention of significant primary space during physical disturbances as well as permitting (2) a more rapid recovery to predisturbance abundances following damage. However, until new fertile uprights are produced, the crustose bases remain sexually and asexually inactive (Dayton 1975).

In his classic paper, Dixon (1965) promoted the concept that vegetative propagation and perennation

are of major importance to the long-term persistence of certain algae and cited one patch of the fleshy red alga, *Pterocladia capillacea* (Gmel.) Born. et Thur., that survived in the field for at least 36 years by seasonally perennnating from prostrate basal remnants. When large overstory algae were removed in the northeastern Pacific (Dayton 1975), understory individuals of *C. officinalis* often partially survived when exposed to moderate desiccation, since the encrusting holdfast systems remained alive, but the articulated fronds died and fell off. The same phenomenon is seasonally widespread throughout the Southern California Bight when occasional strong, hot and dry "Santa Ana" winds (from the inland deserts) during the late fall and winter coincide with daytime low tides. The resultant extreme heating and desiccation stress to intertidal *C. officinalis*, causes extensive mortality of the upright fronds (Littler 1980a, Seapy and Littler 1982), whereas the crustose bases survive.

There was a statistically significant (P < 0,001, Fig. 3A) difference between the characteristically low productivity of the crust and the higher rate of the articulated upright form supporting the productivity hypothesis of Littler (1980b). This pattern of low rates for crusts relative to upright algae is widespread, having been recorded by Littler and Murray (1974), Littler and Arnold (1982), Littler *et al.* (1983) and Littler and Littler (1983). All showed that upright algae with relatively larger surface areas in contact with the surrounding medium tend to have greater photosynthetic rates than crustose species with smaller surface/volume ratios. Because of greater exchange area and surfaces oriented to capture light from many angles, the upright articulated portion of *Corallina officinalis* is better adapted to obtain nutrients (Odum *et al.* 1958) and utilize light energy than is the crustose form.

It is apparent that selection pressures for more productive, reproductive and competitive (but physically vulnerable) upright thalli, as well as selection for highly resistant crustose morphologies, are opposing evolutionary forces that have led to divergence and specialization within heterotrichous marine plants such as *C. officinalis*. This same phenomenon is present in highly-differentiated marine macrophytes such as kelps. For example, translocation work (Lobban 1978) and productivity studies (Littler and Arnold 1980) in *Macrocystis pyrifera* (L.) C. Ag. suggest that the sporophyll blades function as sinks for photosynthate that is produced by more photosynthetically-active source blades. Morphologically differentiated fronds on the same thalli of *Halidrys dioica* Gardner and *Egregia menziesii* (Turn.)

Aresch. have significantly different photosynthetic performances (Littler and Arnold 1980), as do undifferentiated juvenile vs. mature *E. menziesii* (Littler and Littler 1980). Also, individual blades of *M. pyrifera* (Clendenning 1971) and *Laminaria digitata* (Huds.) Lamour. (King and Schramm 1976, Küppers and Kremer 1978) show steeply rising photosynthetic rates with increasing distance from the base.

The urchin susceptibility findings (Fig. 3B) support the predation hypothesis and coincide with the studies of Slocum (1980), Lubchenco and Cubit (1980), Dethier (1981), Littler *et al.* (in press) and Littler and Littler (1983) all of whom substantiated that crustose forms are relatively resistant to conditions of high herbivory. The dramatic difference shown when crustose and upright articulated portions were presented to starved *Strongylocentrotus purpuratus* is due to the much greater ease in which the distally-compressed cylindrical segments (intergenicula, Fig. 1) can be torn free and taken in through the lantern apparatus into the buccal canal. The saxicolous habit and relatively high penetration resistance of the crust (Fig. 4A) resists the scraping action of the teeth, whereas the short intergenicula can be ingested with very little scraping required.

There was no significant difference in calorific content between the basal crust and the upright portion of *Corallina officinalis* (Fig. 4B) in agreement with the findings of Littler *et al.* (1983) for tropical jointed calcareous vs. crustose algae in Belize, Central America. Both portions were quite low in calorific values per unit of organic matter compared to fleshy algae (see Paine and Vadas 1969, Littler and Murray 1978, Littler and Littler 1980, 1983), even when compensated for the high ash content. Macroalgae such as *C. officinalis*, that contain a high proportion of structural $CaCO_3$, presumably of selective advantage in interference competition for space and light or protection from grazing or physical disturbance, have relatively less energy to allocate toward growth and reproduction and tend to produce thalli with lower total calories per unit weight. The low values for both the articulated and basal portions support the contention of Paine and Vadas (1969) that calcification and low calorific content may be important for survival under high grazing pressure by decreasing the energetic yield to herbivores. Alternatively, Littler and Littler (1983) present evidence that the crustose algal phases (and possibly many articulated turf forms, unpublished) are also adaptive as resisters of sand-scour and wave-shearing or physiological stresses such as desiccation and heating. Littler (1976) proposed five hypotheses concerning the ad-

aptive features of skeletal carbonate in marine macroalgae. One interesting idea was that by cementing and stabilizing the substrata, calcareous crustose forms have the unique ability to optimally modify their own microhabitats.

Interest in dealing with marine macroalgae from a functional-group perspective (Littler 1980b) has increased recently. The assumption is that given sufficient understanding of form-function groupings, ecologists may be able to use them as indicators for interpreting patterns as well as to identify environmental or biotic causal relationships without having to laboriously study the individual species. As a maricultural application [e.g. biomass-energy conversion programs (Jackson 1980)], the functional-form relationship could be useful in identifying: (1) potentially productive species, (2) the highest producing stages in the development of differentiated algae, (3) the most productive alternates of an algal life-history having dissimilar morphological phases or (4) the more useful portions of a heterotrichous plant thallus. As predicted by the functional-form model and demonstrated by Littler and Littler (1983), species with heteromorphic generations such as *Scytosiphon lomentaria* (Lyngb.) Link, can not be neatly placed into a single functional group. This study documents the same phenomenon; however, in the case of *Corallina officinalis*, an individual heterotrichous plant concomitantly exhibits divergent form-function attributes.

Continued outward radiation by the basal crust gives *C. officinalis* considerable advantage over non-heterotrichous algae in sequestering primary space. The crustose portion spreads laterally by means of apical cell divisions along the margins and continues producing new uprights if conditions remain favorable. For example, *C. officinalis* on the Atlantic coast of North America (Harlin and Lindbergh 1977) apparently can extend itself indefinitely as a smooth crust until stimulated (e.g., by substratum texture) to develop erect fronds. The upright portions have a decided competitive advantage in exploiting light and nutrients relative to strictly crustose species. Such proliferation from prostrate epilithic portions of marine macroalgae is of widespread occurrence, being present in Phaeophyta (e.g., *Ascophyllum, Pelvetia*), numerous other articulated corallines (e.g., *Calliarthron, Lithothrix*) as well as many fleshy Rhodophyta (e.g., *Chondrus, Gigartina, Polyides*), and should not be overlooked in ecological studies.

In conclusion, we suggest that dissimilar morphological phases within an algal life history or heterotrichy within a single plant have been selected by opposing forces that have resulted in dramatic divergences, and the resultant products function as options that spread the risk from different sources of mortality.

Acknowledgements

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