

HETEROMORPHIC LIFE-HISTORY STRATEGIES IN THE BROWN ALGA *SCYTOSIPHON LOMENTARIA* (LYNGB.) LINK¹

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ABSTRACT

The adaptive significance of a life-history strategy, expressed as divergent morphological forms, was examined for the heteromorphic alga *Scytosiphon lomentaria*. Successional studies were performed by physically clearing mature, temporally-constant intertidal communities on San Clemente I., California. At week six, after clearing, complanate thalli dominated the successional plots (mean cover = 23.5%) and began to decline as the cylindrical form became abundant. The latter attained its peak cover (82.3%) at week 13, whereupon it too began a precipitous reduction. The crustose ralfsioid form appeared surprisingly early (4-13 wks) in trace amounts but did not achieve its greatest cover (85.0%) until week 43. The ranking from high to low primary productivity (cylindrical form = 8.1 mg C·g dry wt.⁻¹·h⁻¹, complanate form = 6.5 mg, crustose form = 0.5 mg) corresponded closely with the data for photosynthetic vs. structural components (cylindrical = 92.3% pigmented, complanate = 65.3%, crustose = 32.0%). This finding indicates that selection in the crust form, which is more readily accessible to epilithic grazers, has tended to increase allocation of materials to nonpigmented structural tissue at the expense of photosynthetic tissue and reduced production rates. The results for thallus losses to urchin grazing over 48 h were complanate form = 82.7% lost, cylindrical = 81.4% and crustose = 16.2%, which correlates with the calorific contents of the three forms (i.e. complanate = 4.97 kcal·ash-free g dry wt.⁻¹, cylindrical = 4.46 kcal and crustose = 3.55 kcal). The crustose form had tougher thalli (26 g·mm⁻² to penetrate thallus) than either the complanate form (12 g) or the cylindrical form (15 g). It is likely that opposing selective factors have resulted in the evolutionary divergences observed in algae with heteromorphic life histories. Previous work may have overemphasized the selective role of grazing because the crustose form is also adapted to withstand physical forces (sand-scouring, burial and wave-shearing) or as an overwintering stage under physiologically stressful conditions.

Key index words: heteromorphic life-history; recolonization, brown algae; *Scytosiphon lomentaria*

Most members of the Phaeophyta show an alternation of morphological generations. Usually there are two generations that may be either isomorphic or heteromorphic. Such life histories were recognized very early as major taxonomic features and used (Kyllin 1933) to classify brown algae at the higher

levels (classes). However, only recently has the adaptive significance of an alternation of heteromorphic generations been considered. An early ecological hypothesis (Neushul 1972) dealt with hydrodynamic constraints on alternate heteromorphic stages of large kelps. Among the first evolutionary interpretations was the suggestion (Vadas 1979) that heteromorphic life histories may have resulted from simultaneous bimodal selection pressures toward the extreme ends of a continuum (see Pianka 1970, r-K selection).

Data confirming the adaptive importance of life histories with dissimilar morphological (somatic) forms has been forthcoming subsequently. Littler and Littler (1980), Lubchenco and Cubitt (1980), Slocum (1980) and Dethier (1981) all have corroborated the greater resistances of crustose life-history phases to herbivory; whereas, the upright stages tend to be more productive (Littler and Littler 1980) and faster growing. Lubchenco and Cubitt (1980) characterized dissimilar alternate stages as mutually exclusive adaptations that have evolved in response to seasonal extremes in grazing pressure. In contrast, Littler and Littler (1980) and Dethier (1981) presented evidence that the various morphological phases are not mutually exclusive and may actually represent options that spread the risk from different sources of mortality ("bet-hedging," see Cohen 1966).

As pointed out by Dethier (1981), the status of the cosmopolitan *Scytosiphon lomentaria* complex is confused. Both *S. lomentaria* (cylindrical), as well as *Petalonia fascia* (Müll.) Kuntze (flattened), produce zoospores (zoids) that give rise to ralfsioid crusts taxonomically indistinguishable from *Ralfsia* spp. (Wynne 1969). There are at least two other documented forms of *S. lomentaria* (besides the cylindrical and crustose thalli, see Fig. 1); i.e. filamentous tufts (plethysmothalli) are produced under certain culture conditions (Wynne 1969, Clayton 1976a, b, Wynne and Loiseaux 1976), and an additional flat (complanate) form of the cylindrical *S. lomentaria* occurs under short-day conditions (Clayton 1976a, b, 1981). The complanate phase is internally hollow (Fig. 1), but otherwise has the same morphology as *P. fascia* (which also can be at least partly hollow like *Scytosiphon*), and is indistinguishable from *S. complanatus* (Rosenvinge) Doty except for the presence of paraphyses (Pedersen 1980). The *S. lomentaria* complex, therefore, portrays an enormous polymorphic variability.

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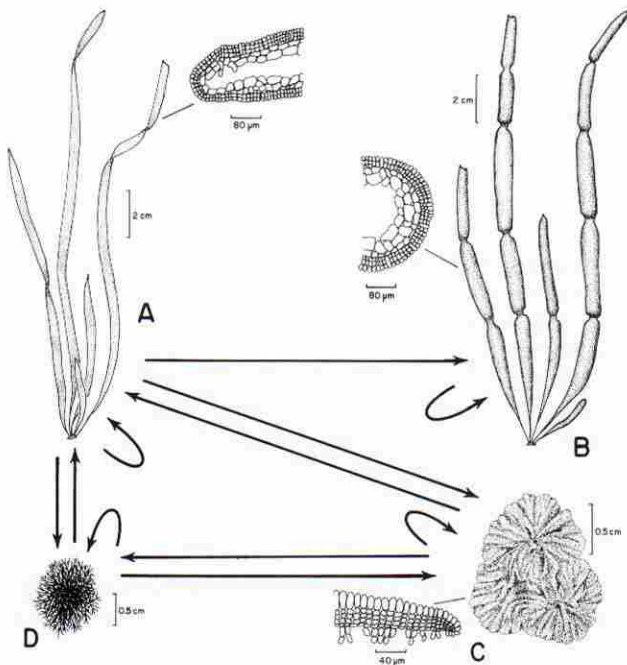


FIG. 1A–D. Life history (after Clayton 1976a, b) and anatomical (cross-sectional) features (present study) of the *Scytosiphon lomentaria* complex. A = complanate form, B = cylindrical, C = crustose and D = filamentous plethysmothalli.

There is no obligate alternation between the various stages or forms (Wynne and Loiseaux 1976), although environmental cues such as temperature and daylength acting on zoid development control their phenology in culture (Wynne 1969, Rhodes and Connell 1973, Dring and Lüning 1975) as well as in nature (Clayton 1981, Dethier 1981). All of the forms can produce zoids that give rise to more of their own thalli (Fig. 1), the zoids of the complanate form can lead to all thallus types whereas those of the ralfsioid crust yield all but the cylindrical form. Depending on age and environmental conditions (Clayton 1981), both of the upright forms become gametophytic while the crust remains sporophytic.

Unfortunately, the suggested adaptive significance of this morphological flexibility in the *S. lomentaria* complex has only been examined with respect to herbivory (Lubchenco and Cubit 1980, Dethier 1981). In the present paper, we investigate both the upright cylindrical and complanate thalli as well as the crustose form from a multi-faceted physiological-ecological-morphological perspective.

MATERIALS AND METHODS

Algal material. Both cylindrical and complanate forms of *Scytosiphon lomentaria* were easily collected during winter through early summer on San Clemente I. and were characteristic of recently overturned rocks. The crustose form (indistinguishable from *Ralfsia californica* Setch. & Gard., the known alternate of *S. lomentaria*, Wynne 1969, Dethier 1981, and vegetative *R. confusa* Hollenberg) was present throughout our studies as a monoculture

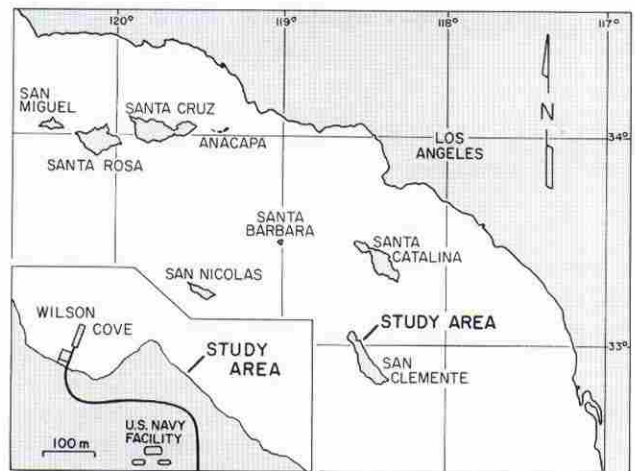


FIG. 2. Location of the study site on San Clemente Island, California.

of overlapping and coalescent discs on unstable boulders. The upright forms usually were found arising directly out of the ralfsioid crusts.

The forms of *Scytosiphon lomentaria* are amenable to field study (e.g. Lubchenco and Cubit 1980, Dethier 1981) due to the detailed morphological-anatomical descriptions and illustrations that are available as a result of an exceptional wealth of culture studies (Wynne 1969, Dring and Lüning 1975, Wynne and Loiseaux 1976, Clayton 1976a, b, 1978, 1981, Pedersen 1980, Lüning 1980). Consequently, it was possible to taxonomically assign each of the three sympatric forms to the appropriate life history phase of the *Scytosiphon lomentaria* complex (Fig. 1). Our voucher specimens are housed in the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution and are available for re-examination by interested workers as follows: cylindrical *S. lomentaria*—No. 080546, complanate—No. 091179 and ralfsioid—No. 091178. This material was compared critically and related to the following original specimens (U.S. National Herbarium): *S. lomentaria* f. *cylindricus* Setch. & Gard.—No. 57012 (Syntype), *S. lomentaria* f. *complanatus* Setch. & Gard.—No. 57010 (Isotype), *Ralfsia californica* Setch. & Gard.—No. 065838 and *R. confusa* Hollenberg—No. 62245.

Our methods were designed to examine the general hypothesis that the divergent physiological, ecological and morphological responses of *Scytosiphon lomentaria* represent a life-history adaptation. The various morphological forms should reflect quite different survival strategies in terms of trade-offs between capacities for rapid growth and productivity, environmental tolerance, resistance to predation and competition (for nutrients, space and light). This prediction was assessed by directly measuring succession, productivities, calories, anatomical features, predation-tolerances and physical qualities of the various forms during laboratory and field experiments.

Study area. San Clemente I. is owned by the United States Navy which maintains an operational base near the study site at Wilson Cove (Fig. 2). Because 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 collecting site (Fig. 2), located approximately 550 m to the south of the southern promontory delineating Wilson Cove (33°00'06" N, 118°33'03" W), is shielded from prevailing winds and waves. The shoreline consists of large granitic boulders mixed with numerous loose rocks (20- to 50-cm in diameter) that provide a habitat mosaic of crevices and angled surfaces over a tidal range of 2.7 m (horizontal distance of 10–15 m).

Successional data. We re-examined voucher and photogram-

metric samples previously obtained (Murray and Littler 1978) from the same study area. At that time, the complanate form studied here was tentatively referred to *Petalonia fascia* based only on external morphology. However, this entity was anatomically the same taxon as the complanate, hollow (with paraphyses, Fig. 1) material studied here and we now attribute it to *Scytosiphon*. Four 20 × 50-cm permanently marked plots were cleared, sterilized and sampled for percent cover of the three thallus types. The study was initiated in early winter (December 1974) between the interval +0.15 and +0.45 m relative to mean lower low water in an undisturbed rocky-intertidal community dominated by macroalgae (Littler and Murray 1975). Subsequent recolonization was measured for the next 129 weeks by the photogrammetric technique given in Littler (1980a).

Productivity data. Measurements of net photosynthesis were made (six whole-thallus replicates for each of the three thallus forms) on San Clemente I. between 0900 and 1400 h during July 1981, at 16.0° C under overcast skies of about 900 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ P.A.R. Net productivity was calculated as milligrams C fixed·g dry wt.⁻¹·h⁻¹ from measurements of oxygen flux (assuming a P.Q. of 1.00). The methods were those of Littler (1980b). For the crustose form, rock fragments containing 5–11 confluent thalli were cleared of other plant materials and animals by scraping with a knife. Several control rocks with no radioid crusts were treated this way and confirmed that the scraping was effective in eliminating measurable production or respiration when the stones alone were incubated. Ash-free dry weight was determined for representative crusts after they were removed from their rock substrata prior to drying. The dried material was then ignited at 500° C to constant weight in a muffle furnace.

Calorific data. Samples of all three forms were collected during July 1981 and returned to the laboratory where they were quickly dipped in distilled water to remove salts. Epibionts were never present. The entire thalli were then dried to constant weight at 80° C, ground to a fine powder in a ball mill, pelletized and three replicate pellets were 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, determined on single aliquots of the homogeneous milled samples (dried at 80° C) by igniting the material at 500° C until constant weight.

Predation data. *Strongylocentrotus purpuratus* Stimpson, a herbivore known to have a broad diet (Vadas 1977, Littler and Littler 1980, Sousa et al. 1981), was used to assess the resistance to predation of the three algal forms. This sea urchin occurs in upper intertidal pools in southern California where it frequently (personal observation) encounters all of the forms examined. Experiments were run during July 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 (ca. 4 cm test diameter), 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 algae were collected from San Clemente I. while submerged and returned immediately to the laboratory where they were separated into preweighed clumps of rock fragments of equal, projected thallus area (3 × 4 cm). Care was taken to ensure that the specimens were not desiccated or mechanically injured. The crustose thalli were used intact on thin fragments of the natural rock substratum. The three algal forms, on a grid (37 × 47 cm) containing 12 clumps per form arranged in mechanically randomized patterns, 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 measure losses of weight other than by grazing. After 48 h on the bottom of the aquarium, the blotted weight of each replicate was determined to ascertain the percent lost to grazing.

Structural vs. photosynthetic tissue. Cross-sections approximately one cell thick were made by freezing microtome for 10 different

specimens of all the three forms. The cylindrical and complanate thalli were also examined directly. The percent pigmented (plastids) and nonpigmented areas were calculated from fresh material with an ocular grid and a Wild M20 fluorescence microscope, which precisely revealed the location of the red-fluorescent pigmented plastids. Point-intercept transects across each specimen were scored with a minimum replicated sample size of 100 intercepts.

Penetration data. Because of the small individual size of the crusts (<15 mm diameter), a penetrometer smaller than that of Littler and Littler (1980) was used to measure penetration resistances of the three thallus forms. The crustose thalli were carefully lifted with a thin palette knife from the underlying substrata. The middle portions of fronds were gently clamped between two acrylic plates across 3.0 mm diameter holes that were precisely aligned on both plates. A cylindrical steel plunger 2.9 mm in diameter with blunted edges, attached below a 0.5 L plastic cup, was carefully placed vertically through the hole in the upper plate so that it rested on the algal thallus. Clean sand was then gently added to the cup until the plunger penetrated the thallus, at which time the total weight of the device was recorded. Different individuals were analyzed for each determination and 25 replicates were run for each of the three forms.

RESULTS

Grazers were never observed in the four successional quadrats (plots were located in the middle of an otherwise undisturbed algal-turf dominated community), and since virtually no lateral encroachment was noticed, we concluded that recruitment by the *Scytosiphon lomentaria* complex occurred from zooids. During the first three weeks following clearing and sterilization, the plots were repopulated by colonial diatoms, blue-green algae and ectocarpoid-like tufts of brown algae, possibly the filamentous plethysmothalli of *S. lomentaria* (Fig. 1, see Clayton 1976a, b). At six weeks (Fig. 3), the complanate form dominated the cleared area with a mean cover of 23.5% and began to decline as the cylindrical *S. lomentaria* became abundant. The cylindrical form attained its peak (82.3% cover) at 13 wk, whereupon it too began to show a precipitous decline. The crustose thalli appeared early (4–13 wk) in trace amounts but did not achieve their greatest cover (85.0%) until week 43, when they began to decrease as canopy-forming perennial Phaeophyta [*Egregia menziesii* (Turn.) Aresch.] and Rhodophyta [*Gigartina canaliculata* Harv., *Corallina officinalis* var. *chilensis* (Dec.) Kütz.] overgrew them. The three forms each dominated in turn, then disappeared from the successional sequence at the following periods: complanate form—17 wk, cylindrical form—26 wk, crustose form—129 wk.

The ranking from high to low apparent photosynthetic rates (Fig. 4A, $n = 6$) was as follows: cylindrical form (8.1 mg C·g dry wt.⁻¹·h⁻¹), complanate form (6.5 mg) and crustose form (0.5 mg). The first two were not significantly different from each other, but both were statistically greater [$P < 0.05$, Eberhardt (1968) method] than the crust.

The calorific values (Fig. 4B) for the three morphological types, from highest to lowest were com-

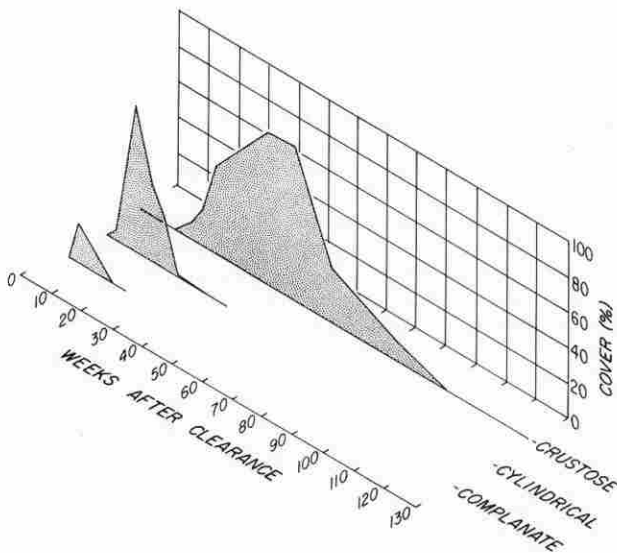


FIG. 3. Successional patterns for the three algal forms (data from Murray and Littler 1978).

planate form ($4.97 \text{ kcal} \cdot \text{ash-free g dry wt.}^{-1}$), cylindrical form (4.46 kcal) and crustose form (3.55 kcal). Each of the means was significantly different ($P < 0.05$, $n = 3$) from all others.

The data for thallus losses to urchin grazing over a 48 h period (Fig. 4C) were complanate form (82.7%), cylindrical form (81.4%) and crustose form (16.2%). The last was significantly lower ($P < 0.05$, $n = 24$) than either of the upright thalli which were not significantly different ($P > 0.05$) from each other.

The crusts (Fig. 4D) contained the lowest proportion of photosynthetic components (32.0% pigmented) in comparison to the complanate thalli (65.3%) and the cylindrical thalli (92.3%). All means were significantly different ($P < 0.05$, $n = 10$). These data correspond closely with the observed pattern of apparent photosynthetic rates (Fig. 4A).

The crust (Fig. 4E) had significantly ($P < 0.05$, $n = 25$) tougher thalli ($26 \text{ g} \cdot \text{mm}^{-2}$ to penetrate thallus) than either the cylindrical form (15 g) or the complanate form (12 g).

DISCUSSION

Both of the upright forms grew rapidly to dominate the early community and then disappeared, leaving the ralfsoid crust and juvenile thalli of relatively long-lived macroalgae (see Murray and Littler 1978 for details). Long-lived seaweeds increased in size until their bases and holdfasts ultimately overgrew and eliminated the crustose form. Although our study was initiated during winter, a similar study nearby (Emerson and Zedler 1978) showed that *Scytosiphon lomentaria* rapidly colonized newly cleared areas throughout the year in southern California, with a maximum response following clearing in summer. This developmental sequence conforms to var-

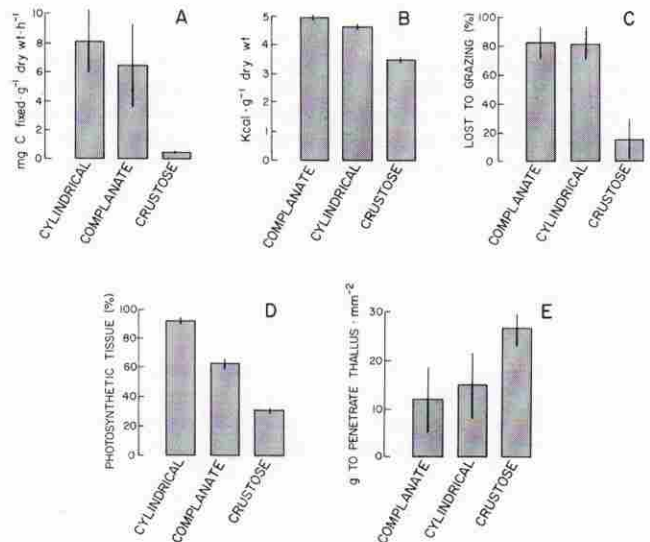


FIG. 4A-E. A. Mean net primary productivities for the three algal forms ($n = 6$). Ash-free data were used for the crustose form. Lines indicate $\pm 95\%$ confidence limits. B. Ash-free calorific values ($n = 3$). C. Resistances to urchin grazing ($n = 24$). D. Percent photosynthetic components ($n = 10$). E. Penetration resistances ($n = 25$).

ious successional models (e.g. Connell 1975, Littler and Littler 1980) which predict that patches disturbed within relatively constant environments dominated by mature communities will be colonized first by species having long reproductive seasons, large numbers of reproductive bodies, rapid growth rates, high productivity and simple thalli with large surface area to volume ratios (see also Littler and Murray 1975, Littler 1980c). The unexpectedly early appearance of the crustose form within one month after clearing agrees with the observations of Dethier (1981).

There was a statistically significant ($P < 0.05$, Fig. 4A) separation between the relatively low production rates of the crust and the two upright forms, supporting the productivity hypothesis of Littler (1980c). The highly productive upright thalli are better adapted to utilize light energy and obtain nutrients (Odum et al. 1958) than is the crustose thallus. This difference is due to greater exchange surfaces and differential allocation of resources and energy to photosynthetic, as opposed to structural, tissues (Fig. 4D). It is likely that selection pressures for delicate thalli with rapid growth, as well as selection for tougher and more persistent morphologies containing considerable structural tissues, are opposing evolutionary forces that could have led to divergence, and hence heteromorphic phases, within algae such as *Scytosiphon lomentaria*.

The significantly lower calorific values for the crust vs. upright forms (Fig. 4B) agree with data for other species from temperate (Paine and Vadas 1969, Littler and Murray 1978) and tropical (Littler et al. 1983a) ecosystems. The two upright thalli, contain-

ing a high ratio of photosynthetic to structural tissue (Fig. 4D), have relatively more energy to allocate toward rapid growth and reproduction and tend to have higher total calories per unit weight (Fig. 4B). In contrast, the crustose form shows lower production (with associated reduced surface to volume ratios, see Odum et al. (1958), Littler and Littler (1980)) and tends to have lower calorific values. Our calorific numbers in conjunction with the predation resistance data (Fig. 4C), corroborate the suggestion (Paine and Vadas 1969, Littler 1976) that crustose algae, which are easily accessible, may have reduced their appeal to herbivores through evolution of thalli that are relatively tough (Fig. 4E) and low in nutritive content.

The urchin-resistance data (Fig. 4C) are in accordance with the predation hypothesis of Littler and Littler (1980) and the field studies of Slocum (1980), Lubchenco and Cubit (1980) and Dethier (1981) all of whom recorded that crustose species are adapted to conditions of high herbivory. As shown by Dethier (1981), the *Ralfsia californica* stage, which is the same entity as our crustose form, requires moderate levels of grazing to avoid overgrowth by superior competitors that do better lower on the shore. Our findings also agree with research (Lubchenco 1978) involving the generalist snail *Littorina littorea* L. which preferred delicate algae such as *Petalonia* and *Scytosiphon*; these were cited as apparently lacking either structural or chemical means of deterring herbivores.

Lubchenco and Cubit (1980) have postulated that heteromorphic algal life histories have been selected by seasonally variable but predictable grazing pressures; the upright fast-growing phase should be present during seasons of low herbivory and the grazer-resistant but competitively inferior crustose stage during the remainder of the year. On the contrary, however, the crustose *Ralfsia californica* alternate has (Dethier 1981) at least three characteristics that are clearly at odds with the hypothesis: (1) its peak abundance occurs at the season of lowest herbivory, (2) it rapidly colonizes new substrata and reproduces year round and (3) the *Ralfsia-Scytosiphon* complex does not partition the year in any way. The most likely interpretation (Littler and Littler 1980, Dethier 1981) is that heteromorphic life history phases are not mutually exclusive, but represent "bet-hedging" evolutionary strategies in the macroalgae.

One particularly disturbing factor in nearly all of the previously published grazing studies is that they invoke herbivory as the primary force selecting for heteromorphic life histories. Alternatively, we suggest, based on our field observations throughout the Southern California Bight, that the crustose phases of many algae also represent functional adaptations to resist sand-scouring, burial and wave-shearing or as overwintering stages under harsh environmental conditions that exceed the physiological resiliencies (homeostasis) of the more delicate upright stages.

Circumstantial evidence in partial support of this statement comes from San Nicolas I., California, which receives periodic sand inundation of the rocky intertidal system near Dutch Harbor during the winter months (Taylor and Littler 1982, Littler et al. 1983b). The ralfsioid crust is always abundant in this system even when sand cover approaches 100%; however, upright *Scytosiphon lomentaria* thalli are only present when sand cover averages below 20%. As sand moves off the intertidal bench, cylindrical *S. lomentaria* uprights appear to germinate on (or from) the crustose form, but are torn back to remnant abraded portions that ultimately die when sand inundation again becomes extensive (~5–40% sand cover). Lüning (1980) has proposed, from growth studies in culture, that the crust phase represents the form best adapted to survive severe winter conditions at northern latitudes as well as high summer temperatures toward the south. Therefore, herbivory, while clearly an important factor, may have received a disproportionate emphasis (Slocum 1980, Lubchenco and Cubit 1980, Dethier 1981), because sand-scouring and wave-shock (forms of physical disturbance) as well as physiological stresses (e.g. desiccation, burial and temperature) probably play a selective role in other intertidal habitats (e.g. San Nicolas I.) and certainly are worthy of further attention.

Our findings, which contrast sheet-like and tubular forms of *Scytosiphon* with the crust form (i.e. opposite ends of the spectrum), are consistent in every respect (Figs. 3, 4) with the functional-group concepts (Littler 1980c, Littler and Arnold 1982, Steneck and Watling 1982, Littler et al. 1983a). However, when the ralfsioid form (Crustose-Group of Littler 1980c) is examined relative to predictions implicit in the functional-group approach, it appears to be somewhat enigmatic. For example, Dethier (1981) states that this crust lies in an unusual middle region between opportunistic and late-successional forms, and our successional data concur with this interpretation. It is a rapid colonizer on new surfaces, relatively short-lived (7–12 mo lifespan), reproduces constantly and is a poor competitor (Dethier 1981). However, in comparison with the upright forms, it also has high herbivore resistance (or even dependence, Dethier 1981), low calorific values and relatively low photosynthetic to structural tissue proportions along with concomitantly reduced production rates, characteristics associated with species prevalent in mature communities.

The resolution of this seeming contradiction lies in a close morphological examination of the ralfsioid form and a critical comparison with other crustose species for which a parallel body of knowledge exists. Although it possesses a crustose morphology, the ralfsioid form is relatively thin (~300 μm) even when contrasted with the upright cylindrical and complanate forms. Therefore, it probably represents one extreme within the Crustose-Group (Lit-

tlter 1980c) since most members of that assemblage tend to be heavily-calcified (e.g. crustose Corallinaceae) or much thicker (e.g. *Pseudolithoderma nigra* Hollenberg). Steneck and Watling (1982) dealt with this problem by including such non-calcified crusts within the intermediate Thick Leathery-Group. Some support for this reasoning is provided by comparisons with all other members of the Crustose-Group for which there are published data. Relative to the means for other crustose algae (primarily calcified species), the much thinner ralfsioid form averages (1) twice as high in productivity, (2) 16 times higher in palatability, (3) 1.3 times higher in its photosynthetic to structural tissue ratio and (4) 4.7 times higher in calorific value, but is (5) biomechanically only 7% as tough. Comparable figures contrasting literature data for only non-calcified members of the Crustose-Group are: ralfsioid form = 1.5 times higher in productivity, and about 55% lower in toughness (penetration resistance). Possibly the best interpretation is that the ralfsioid form is specialized for habitats that are physiologically stressful and periodically disturbed (see also Dethier 1981), and such specialization has pulled it away from easy categorization in any general scheme. We conclude that the functional-group ranking (Littler 1980c) realistically should be regarded as recognizable units along a continuum, each containing considerable variations of forms and concomitant functional responses.

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THE BOTTOM-ICE MICROALGAL COMMUNITY FROM ANNUAL ICE IN THE INSHORE WATERS OF EAST ANTARCTICA¹

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ABSTRACT

The structure, productivity and heterotrophic potential of an extensive microalgal community growing on the underside of sea ice near the Australian Antarctic Station of Casey, are described. Underwater observations made near the Australian Antarctic stations of Davis and Mawson are also reported. This community develops during September, is largely suspended from the bottom surface of annual sea ice and often extends into the underlying water column as conspicuous strands up to 15 cm long. The algal community structure in the strands is dominated by an unidentified tube diatom belonging to the *Amphipleura*/*Berkeleya* group and chains of a species of *Entomoneis* cf. *Amphiprora paludosa* var. *hyperborea* (Grunow) Cleve. Unlike previously described bottom ice environments, a brash ice layer under the hard sea ice is absent. Living cells, predominantly *Nitzschia frigida* Grunow, also occur in microbrine channels in the bottom 3 cm of the ice. Maximal primary production rates of $81 \mu\text{g C} \cdot \text{L}^{-1} \cdot \text{h}^{-1}$ occurred during November, then began declining near the end of December. Minimal rates ($2.8 \mu\text{g C} \cdot \text{L}^{-1} \cdot \text{h}^{-1}$) were reached in mid-January and coincided with changes in the physical structure of the sea ice and in the stability of the water column. An abundant epibacterial community associated with the microalgal strands assimilated ³H-labelled amino acids suggesting significant heterotrophic recycling of dissolved organic matter. Turnover times of assimilated amino acids in the bottom ice community averaged 55 h during November while negligible turnover of these substrates occurred in the water column

1.5 m below the ice. These bottom ice communities have higher primary productivity than typical brash ice communities; they are also accessible to marine herbivores and so may be more important to the Antarctic marine food chain than previously supposed.

Key index words: Antarctic; bottom type community; heterotrophic turnover; primary productivity; sea ice algae; tube diatom

Microalgal communities associated with Antarctic and Arctic sea ice are important to the primary productivity of the polar oceans. Not only do ice algae produce considerable amounts of organic matter but the extensive growth that occurs during spring and autumn, when water column photosynthesis is negligible, extends the short polar growing season (Bunt 1968, Allen 1971, McRoy and Goering 1974, Horner 1976, 1977, Bradford 1978). The most extensively studied sea ice communities are those on the undersurface of the ice; populations of microalgae have also frequently been observed near the surface of Antarctic sea ice (Burkholder and Mandelli 1965) and more rarely within internal layers (Hoshiai 1972, Ackley et al. 1979).

In the Arctic, bottom-ice communities develop during the late spring (April–May) in response to increased solar radiation. The microalgae form a colored layer (1 to 4 cm thick) in the bottom layer of the sea ice and tend to grow between vertically orientated ice platelets rather than on the flattened undersurface itself (Meguro et al. 1967, Alexander et al. 1974). Communities on the undersurface of

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