SAMPLING AND INTERPRETIVE CONSIDERATIONS IN THE MEASUREMENT OF MACROPHYTIC PRIMARY PRODUCTIVITY: AN OVERVIEW WITH RECOMMENDATIONS

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ABSTRACT

To standardize the data in comparative productivity studies, macrophyte weight/volume ratios should be optimized, while assuring that the specimens used are representative of the organism being investigated. It is better to incubate one, or a few individuals in a smaller bottle than to use many thalli in a larger bottle. For comparative purposes, it is imperative that thallus dry weight/volume ratios be reported. It is just as important to specify the incubation time so that the magnitude of changes in O_2, CO_2, and pH can be calculated in comparative studies. Some means of agitation is required to obtain realistic production rates in closed containers. Bubble formation can be problematical, depending upon the bubble volume and the extent to which the gas and liquid phases are in equilibrium. Additionally, O_2-electrode data should ideally be supplemented with some other method (e.g., pH, ^{14}C, Winkler) when experiments are to be conducted at high O_2 levels. Supplementation with the pH or ^{14}C technique would have the added advantage of providing an estimate of PQ. It is clear that estimates of productivity based on light/dark containers will vary as a function of (1) the O_2 concentration used, as well as (2) the relative reactions of photosynthesis and dark respiration to different O_2 tensions. Comparative field studies should be made under uniform conditions of initial dissolved O_2, and the initial tensions of the light and dark bottles must be given.

Depending on the objectives and questions being asked, the kinds and ranges of variability due to season, age, reproductive condition, morphology, thallus portion, crowding, macrohabitat, microhabitat, desiccation and physical stress must be taken into account when designing studies on marine macroalgal productivity. This is equally essential for both field and laboratory studies, and much of the published research should be reassessed in light of the differences demonstrated.

INTRODUCTION

Many of the studies on primary productivity of marine macrophytes have not considered the effects of (1) incubation conditions, (2) antecedent environmental differences, and (3) intrinsic aspects of variation within the organisms themselves. The effects of light/dark bottle incubation techniques have now been documented in detail (Littler, 1979), as have differences due to antecedent environmental conditions and intrinsic sources of variability (Littler and Arnold, 1979). In this paper, laboratory and field procedures for measuring macrophyte primary productivity by the electrode methods developed in my laboratory are presented in detail, and the argument is put forth that many of the published measurements and interpretations of macrophytic primary productivity should be reassessed in view of recent information. An understanding of the sources of variation in apparent photosynthetic rates of marine macrophytes is essential in order to (1) make accurate estimates of individual photosynthetic values, (2) determine seaweed contributions to marine productivity, and (3) analyze evolutionary strategies of carbon allocation.

Specifically, this paper summarizes information on the degree to which variations in bottle volume, thallus weight, incubation time, oxygen tension, and mixing rates interact to affect the assessment of macrophytic primary productivity. Also reviewed are the effects of season, age, reproductive status, external morphology, thallus portion, crowding, macrohabitat, microhabitat, desiccation and physical stress. The experimental methods used have been compiled in Appendix A. Both care and attention should be directed to them; they are essential to the central themes of this paper.

Littler, M. M. 1980. Sampling and interpretive considerations in the measurement of macrophytic primary productivity: an overview with recommendations. Pages 62-71, 186-187 in I. A. Abbott, M. S. Foster and L. F. Eklund, eds. Pacific seaweed aquaculture. California Sea Grant College Program, Institute of Marine Resources, University of California, La Jolla, California, U.S.A.

RESULTS AND DISCUSSION

Effects of Incubation Techniques

Bottle Experiments

The ratio of bottle volume to weight of algal material has been shown by Littler (1979) to have a dramatic impact on measurements of apparent photosynthesis in marine macroalgae (figure 1). The primary result is a considerable lowering of rates in the smaller bottles used. Much of this effect has been attributed to depletion of nutrients (e.g., Buesa, 1977), or excretion of auto-inhibitory substances (Findenegg, 1965), with little supportive data. A more plausible explanation (Dromgoole, 1978a; Littler, 1979) may be that carbon is depleted earlier at the higher weight to volume ratios.

Buesa (1977) examined the production rates of Thalassia testudinum Banks ex Konig and Caulerpa cupressoides (West) C. Ag. in 77, 286, 546, and 1214 ml bottles using mean thallus weights of 0.16 g/l for T. testudinum and 0.12 g/l for C. cupressoides. Although the same ratio of plant material to seawater was consistently maintained regardless of bottle size, Buesa (1977) obtained net photosynthesis and dark respiration values in the 77-546 ml bottles that were only about one-half those obtained in the 1214 ml bottles for both species. The cause of the bottle-size effect recorded by Buesa remains obscure and would not be easily attributable to a surface bacteria effect (Hepher, 1962) because of the relatively large ratio of photosynthesis/respiration in marine macrophytes. Perhaps to maintain the constant algal weight/volume ratios in the smaller bottles, Buesa had to use torn or cut fragments of thalli, which has been shown (Unesco, 1973; Hatcher, 1977) to lower production rates in some marine algae. It is clear that studies in the laboratory using very small discs or segments cut from only a few thalli can lead to interpretive problems if such measurements are extrapolated to natural field conditions. For example, cut thalli had to be washed in seawater for several hours prior to measurements (Dromgoole, 1978b), or inordinately large dark respiration values would be obtained. Some of this effect may have been non-biological and due to release of phenolic compounds and their subsequent oxidation (Dromgoole, 1978b).

Lighter thalli in small bottles generally outperform heavier thalli in large jars (figure 1) at both low and saturated levels of initial O_2, peformance at supersaturation was nearly equal in all cases. However, the lower weight/volume ratios should have favored the larger jars (i.e., 0.105 g/l jars vs. 0.116 g/l bottles for Ulva; 0.048 g/l jars vs. 0.097 g/l bottles for Colpomenia). This finding was in marked contrast to the observation of Buesa (1977) and was attributed to competition for nutrients or CO_2 and the mutual self-shading of individual thalli even when surrounded by an ample volume of seawater.

The amount of thallus selected for incubation had a pronounced effect on measured photosynthetic rates (figure 1) for many of the same reasons that bottle volume was important. Wood (1968) recorded decreased photosynthetic values (2-10 fold) as a function of increased amounts of Cladophora incubated, which he credited to light limitations due to self-shadings. Adams and Stone (1973) used roughly double the amount of Cladophora per volume of water that Wood (1968) did, with correspondingly lower photosynthetic rates. Also, a 7-fold increase in photosynthesis of benthic Cladophora populations over a 9-fold range of thallus dry weights/100cm^2 of substratum was reported by Pfeifer and McDiffett (1975). These workers felt that mutual shading of the algal filaments might be as important as nutrient competition or excretion concentration in reducing production.

Buesa (1977) examined the effect of a range of thallus weights (0.004 to 3.80 dry g/l) on apparent photosynthesis for 11 species of marine macrophytes using 1214 ml bottles. The results varied from species to species, but the highest values for both photosynthesis and respiration were obtained when weight/volume ratios were between 0.020 and 0.195 g/l. Inhibition of primary productivity in Ceramium tenuicorne (Kutz.) Waern was recorded (Wallentinus, 1978) as a function of increasing length of incubation time and sample size incubated. For the largest thalli incubated (~0.6 g/l), productivity measured over a 3.0 h period was 50% lower than for the smaller thalli (~0.01 g/l). Thallus concentrations intermediate to these showed ~25% reductions in productivity for 6.0 h vs. 1.0 h incubation times. Johnston (1969) stated that if a tissue to incubation volume ratio of 0.1-0.3 dry g/l were employed, no nutrient or carbon deficiency occurred in experiments lasting up to 24h. I obtained the highest rates of photosynthesis (over 4.5-6.0 h periods) when average thallus weights did not exceed 0.05 g/l of seawater and when thallus areas were kept below

$30cm^2$, irrespective of bottle volume (figure 1).

Continuous Monitoring Experiments

Stirring Effect. The consequences of water movement on measurements of apparent photosynthesis can be striking (table 1). A greater effect was shown for the high producer, Ulva lobata (Kutz.) Setchell and Gardner, than for the low producer Colpomenia sinuosa (Roth) Derbes and Solier, where continuous measurements made over a nonstirred period were considerably lower (73%) than over a period of vigorous mixing. I attribute the difference to concentration gradients within the system; insufficient flow past the electrode is usually not a problem in pH measurements. Such differences are presumably representative of real reductions in photosynthesis due to the build-up of diffusion barriers at the plant/water boundary layer. Kanwisher (1966) observed a doubling of photosynthetic O_2 production following shaking during respirometer studies of marine macroalgae. Buesa (1977) also confirmed a similar response to mixing for marine macrophytes in his report of 34% photosynthetic reductions in nonshaken vs. shaken bottles. The rate of photosynthesis in the marine macroalgae Padina was recorded (Unesco, 1973) to be 61% lower in unstirred vs. stirred bottles. The effects of current flow (2.1 cm/sec) on benthic Cladophora populations (Pfeifer and McDiffet, 1975) led to 12% and 33% increases in net photosynthesis and dark respiration, respectively, over values obtained in still water. Similarly, Whitford and Schumacher (1961) showed that the benthic algae Oedogonium kurzii Zeller had 70% greater dark respiration rates in shaken vs. nonshaken flasks. In the case of Colpomenia sinuosa (table 1), continuous mixing did not result in an increase in photosynthesis over that in still water or intermittent mixing. The difference is probably related to (1) the relatively low surface/weight ratio of Colpomenia (0.2 cm^2/mg vs. 0.6 cm^2/mg for Ulva), which would reduce its uptake and exchange potentials even in vigorous currents and (2) its low productivity, which would result in smaller diffusion gradients than in a high producer such as Ulva.

Bubbles can result from degassing on surfaces (e.g., sides of the container, stir bars, partitions, algal thalli) at warmer temperatures than the seawater or by metabolic O_2 production at high levels of supersaturation. Much of the problem can be avoided by cooling the incubation equipment with ambient seawater prior to use; however, small gaseous bubbles often appear in approximately equal amounts irrespective of initial O_2 concentration. Bubble formation may have serious consequences, depending on the volume of the gas and the extent to which the gas and liquid phases are in O_2-tension equilibrium. However, the formation of bubbles had little effect on Littler's (1979) measurements of dissolved O_2 because both pH and O_2-derived numbers were quite close (figures 2A and 2D).

Oxygen Tension Effects. The effect of variations in dissolved O_2 levels is complex (figure 2). There would seem to be two possible interpretations. First, it has been documented that apparent photosynthesis in marine plants (Downtown, et al., 1976; Black, et al., 1976; Dromgoole, 1978b), as well as dark respiration (e.g., Dromgoole, 1978b), is quite sensitive to O_2 concentration. This photosynthetic decrease under increased concentrations of O_2--the Warburg effect--is considered (Jackson and Volk, 1970; Black, et al., 1976; Burris, 1977) to be an indication of photorespiration. The sensitivity and accuracy of the O_2 electrodes does not decrease as a function of high concentrations of O_2 (i.e., beyond saturation) and has been shown (Beckman Instruments, Inc., 1972) to be linear at O_2 levels in seawater considerably higher than those used in the present research.

Second, the photosynthetic quotient might change with increased O_2 tension, and this very likely contributed to the discrepancy between the two methods. In general, O_2 evolution in marine macroalgae seems to be inhibited by high O_2 tensions (Downtown, et al., 1976; Dromgoole, 1978b), as is ^{14}C uptake (Black, et al., 1976; Burris, 1977); however, this may be highly species specific, since photosynthesis in the marine macroalgae Chaetomorpha sp. was highest under increased O_2 tension (Burris, 1977). Nonetheless, the data (figures 2A, B, C) clearly show not only a reduction in CO_2 uptake at the higher O_2 levels (mean decrease of ~24% as measured by pH) but also a dramatic decline in photosynthetic O_2 production relative to CO_2 uptake at high O_2 levels in sealed containers, indicating a change in the photosynthetic quotient.

Effects of Intrinsic and Environmental Variability

Intrinsic Variation

Seasonality. Littler and Arnold (1979) have documented opposite seasonal patterns between the net primary productivity of Corallina officinalis var. chilensis (Decaisne) Kützing and Egregia menziesii (Turn.) Areschoug from the same intertidal habitat (figure 3). If comparisons were made based only on measurements taken in the summer, E. menziesii would be observed to be the highest producer, whereas October values would yield the reverse interpretation. Littler et al. (1979) concluded that the seasonal patterns of marine macrophyte production are extremely variable, with a tendency for most species to reach their peak daily photosynthesis coincident with higher temperatures and longer daylengths.

Age. The juvenile individuals of the kelp Egregia menziesii (figure 4A) have been shown (Littler and Arnold, 1979) to fix 2.5 times more carbon per gram dry weight than the blade portions of mature fully-differentiated thalli. In the kelps (Laminariales), juvenile sporophyte stages are simple blades with very little structural differentiation (Littler and Arnold, 1980) and a large proportion of photosynthetically active cells. Consequently, and in accordance with the functional form hypothesis suggested by Littler (1980), such young thalli should predictably have considerably higher rates of production relative to mature stages that have allocated much of their biomass to photosynthetically inactive structure.

Reproductive Condition. Significant but opposite differences were noted by Littler and Arnold (1979) between reproductive and vegetative blades of Halidrys dioica Gardner and Macrocystis pyrifera (L.) C. Agardh (figure 4B). Fertile portions of Halidrys had 1.6 times the net productivity and 20% of the respiration of nonreproductive portions. Conversely, the sporophyllis of Macrocystis yielded no measurable net productivity and statistically lower respiration when compared with vegetative blades. It has been noted (Haxo and Clendenning, 1953) that the fertile margins of Ulva lactuca L. have respiratory rates that are two to four times higher than the central vegetative cells and only 50-66% as productive.

External Morphology. The three populations of Gigartina canaliculata Harvey, although from visually similar habitats, had marked differences in photosynthetic rates (figure 4C). The tougher, more wiry populations apparently contained a lower percentage of photosynthetic cells, which decreased their weight-based production rates. In a related study (Peterson, 1972), specimens of Caulerpa racemosa (Forsskal) J. Agardh grew more flattened with higher surface to volume ratios under low light intensity. This resulted in larger gross photosynthesis/respiration ratios and higher net photosynthesis at lower light intensities. Correlations between physiological and morphological plasticity, such as reported by Peterson (1972) and Littler and Arnold (1979), indicate a critical need to understand the adaptive significance of these kinds of variations.

Thallus Portion. The less-differentiated coarse laterals of Egregia menziesii have been observed (Littler and Arnold, 1979) to have double the net productivity and respiration as finer mature laterals from the same plant (figure 4D), indicating that as thalli mature, productivity becomes lower on weight basis because of increases in structural components. Similar gradients from tip to base within individual blades have been measured for E. menziesii (Chapman, 1962). Macrocystis pyrifera (Clendenning, 1971) and Laminaria digitata (Hud.) Lamour (King and Schramm, 1976b; Küppers and Kremer, 1978). As a consequence, such gradients must be carefully considered when extrapolating measurements made on small portions of large complex macrophytes to entire individuals or populations.

Crowding. Separated fronds of Gelidium pusillum (Stackhouse) Le Jolis produced and respired at slighty less than double the rate of the natural turf form (figure 4E). Also, the data presented earlier (figure 1) demonstrated that fewer macroalgal individuals in small bottles consistently produced at higher rates than the more numerous thalli of the same species in large jars, although the lower weight/volume ratios should have led to greater production in the large jars. This was attributed primarily to the mutual self-shading by overlapping thalli even when surrounded by relatively large volumes

of seawater. In a related study (Dawes, et al., 1978), the low productivity of Cladophora was attributed to its clumped habit, a growth form that apparently ameliorates desiccation stress during low tide periods of exposure to air. These data for finely-branched but clumped forms, therefore, represent an exception to the generalization of Odum et al. (1958) that algae with high surface to volume ratios produce more than those with lower ratios. It is likely that selection for resistance to heating, desiccation, or grazing had led to the tightly clumped habits of turf algae (Hay, 1978) which greatly lowers their photosynthetic capacity even though they retain high surface to volume ratios.

Habitat. Photosynthetic and respiratory differences were shown by Littler and Arnold (1979) for Colpomenia sinuosa but not for Codium fragile (Sur.) Hariot (figure 4F). These workers attributed the higher metabolic rates (1.5 and 2.5 times greater for photosynthesis and respiration, respectively) of subtidal Colpomenia to their thinner construction with less self-shading by structural tissue. Although the increase in structure of intertidal populations lowered the photosynthetic performance per unit weight, such morphological responses appear to be adaptive (Littler and Littler, 1980) by conferring greater environmental resistance.

Light Acclimation. Sun forms of Corallina officinalis var. chilensis showed nearly four times the net photosynthetic output as shade forms (figure 4G), no doubt because of photoinhibition in the latter. Photoinhibition has also been shown to be common (Peterson, 1972; Littler, 1973b) when shade-acclimated algae are exposed to high natural light intensities.

Desiccation. Specimens of Halidrys dioica that had been desiccated for 1.0 h had only half the photosynthetic rates of fresh material (figure 4H), although respiration was unaffected. Numerous workers (e.g., Ogata and Matsui, 1965; Champan, 1966; Schonbeck and Norton, 1978) have documented reduced photosynthetic and respiratory rates upon reimmersion after periods of desiccation. Such reductions have been correlated with habitat (Mathieson and Burns, 1971; Schonbeck and Norton, 1978); those species located higher on the shore generally show the greatest ability to regain photosynthetic response following desiccation.

Physical Injury. Littler and Arnold (1979) showed that compression by squeezing nearly doubled respiration in Colpomenia sinuosa while reducing photosynthetic performance by one-half (figure 4I). This observation has serious ramifications on interpreting data from studies where cut discs or torn segments have been incubated and used to extrapolate to field conditions. Respiratory rates and variability among replicates greatly increased in Laminaria longicruris De la Pylaie in cut segments relative to whole plants (Hatcher, 1977). When injured many Phaeophyta leak phenolic compounds (Ragan and Jensen, 1977; Sieburth, 1968; Dromgoole, 1978b), which can become rapidly oxidized and obscure metabolic exchanges of oxygen.

Methodological, intrinsic, and environmentally-related populational variations must be assessed before the production roles of marine macrophytes can be estimated accurately. Much more research, including reliable measurements taken from both warm-water and cold-water systems, is required before we will be in a position to generalize or make precise predictions concerning annual patterns of carbon allocation, or to understand the selective processes that have molded macrophyte production strategies.

ACKNOWLEDGMENTS

The careful assistance of Keith Arnold, Cally Curtis, Andrew Kindig, Mark Hay, Jack Fancher, and Greg Ruggerone is gratefully acknowledged. Sincere appreciation is extended to Diane S. Littler who provided the illustrations and whose critical proofreading further improved the manuscript. I am grateful to Jan Larson who aranged our logistic support by the U.S. Navy on San Clemente Island.

The research leading to this report was supported by the Office of Water Research and Technology, USDI, under the Allotment Program of Public Law 88-379, as amended, and by the University of California, Water Resources Center, as a part of Office of Water Research and Technology Project No. A-054-CAL and Water Resources Center Project W-491.

TRANSCRIPT OF DISCUSSION

DOTY: Dr. Littler's introduction named a lot of potential pairs of independent-dependent factors. These should be studied to see if there are potential cause-and-effect relations and what they are. Those must be taken into consideration when projecting production rates, and they must be utilized in interpretation of the potential environmental effects of doing this or that. This means controlled experiments. Dr. Littler has been doing controlled experiments. It's a refreshing sort of paper to hear. He has been able to create a little environment in that monstrous box that he uses. One of the things that strikes me that we're getting at in these large/small body experiments is that there are many factors that we do not measure when we study the environmental relationships of algal behavior. As students of these phenomena, we should press and try to learn how to measure more of the environmental factors in a practical way. We measure nitrogen and its free forms because it's relatively easy with the machinery that the electronics people give us. It isn't easy chemically, I know. Phosphate we measure: it's easy chemically and with the machines they give us. Oxygen is easy to measure. We measure the easy things, but are they always the important things? I think they aren't, and I think your work is a clear indication that there are other things. Of course, the fish people have been worried about these size problems for a long time. A fish in a little bottle, no matter how much you pump the water through, is not apt to be very happy or grow very large. You can get extremely high production in cages of fish where the fish are almost packed, and if you pour food through. They don't get exercise and they put on weight. Someone might want to comment on your results with Colpomenia and Ulva, their respiration and so forth, with stirring because every cell in Ulva is in contact with the water. In the case of Colpomenia, it is a very different situation.

LITTLER: I had a recent paper comparing standing crop changes with photosynthetic changes over seasons. Generally speaking, the growth and photosynthesis tend to be higher during the warmer times of the year in southern California when the day length is longer and the sun is at a more right angle to the water. That doesn't hold universally true. Standing stock measurements don't account for material lost to the ecosystem due to dissolved organic material production to sporulation, and this may well be applied. Bob Waaland's data for vegetative Gigartina tended to be lower in photosynthetic output, even though it was a fast grower. It probably wasn't losing material as spores and putting more energy into vegetative growth. You have that kind of problem. Then you have losses due to grazing effects in standing stock in the field. Photosynthetic measurements are much more related to the handling of carbon by the organism in a system. You are looking at a different question than you are with growth when you are trying to get a certain yield of material back out. However, the two do come together in an area I'm especially interested in, and that's strategies of carbon allocation in some of these complex seaweeds. We would like to know what these seaweeds do with this initial budget of carbon that they can obtain, how they allocate it, and how one might select some they allocate in different ways, perhaps more useful to cultural type programs, and so on.

NELSON: Since you have shown that there are several factors that will influence the results of your experiments, would it be possible for you to draw up tables to take into account size of the jar, amount of stirring, et cetera, so people have some kind of standard procedure to use for a way of comparing results?

LITTLER: It would be hard to come up with universal figures for that. Generally, the seaweeds that have a high surface area to volume ratio produce at much higher rates than those with lower surface/volume ratios. It goes through a spectrum all the way down to the crust. Those are the low producers. If the person gave the data I indicated--gave the weight/volume ratios, oxygen tension, all those things--you could make some judgments that would allow you to compare. As far as having some universal formula, you can't do it, because of all these sources of variability. If you are going to do comparative studies, you have to do them in a way that optimizes photosynthetic rates, and you have to give the data that would allow somebody to make the judgment. I was interested earlier in Dr. Doty's comment that mature algae tend to grow at about three-to-three-point-five percent/d. They certainly wouldn't photosynthesize at a standard rate like that. They all photosynthesize at different rates, depending on their morphological

form, which is directly related to how much material they allocate to photosynthetic tissue and how much they allocate to structural tissue. For instance, I would expect a crustose coralline alga to grow at a very low rate. Perhaps its photosynthesis is of an order of magnitude lower than that of Ulva. However, I think that what you were referring to, Dr. Doty, was a lot of these aquaculture species that do have similar fleshy type morphology are remarkably similar in their growth rates. They are probably similar in their photosynthetic rates also. If you want to optimize photosynthetic rates the ratio wouldn't exceed about point-four (zero) grams dry weight per liter water. It can't be material that is a whole lot of little pieces that overlap each other and tend to clump in the middle of the jar, because that will lower the rate. It has to be a single thallus at about that ratio. You need to optimize the rates because you want to have something to measure. Incubation times enter in here. If you had more material you would have to incubate a shorter time to get a measurable rate. However, there is a carryover from what the alga has been doing in the previous conditions to what happens after you put it into a bottle. If it has been in bright light photosynthesizing and you put it into a dark bottle, it is going to continue producing oxygen for a while. You can't shorten that incubation time down too short, or you run into those kinds of problems. I would recommend, based on southern California seaweed production rates, no more than point-four (zero) grams per liter and incubation times of around four to six hours on the average. One source of variability is daily photosynthetic periodicity, which Dr. Doty discovered for phytoplankton and which Dr. Blinks couldn't find for seaweeds. We have been looking at it for seaweeds, and we can't find it either for West Coast seaweeds. We find no daily photosynthetic periodicity.

QUESTION: You found the subtidal form of Colpomenia to have higher rates than the intertidal algae. Could that be a function of the higher light levels, etc.?

LITTLER: It's directly attributable to the differences in the form. We are reporting our photosynthetic rates as a function of gram dry weight. On a cm square basis, the intertidal material is much thicker and fleshier, probably to allow it to withstand desiccation. The subtidal material tended to be much thinner, so that when you did production on a surface area basis they were about equal. But on a weight basis, the subtidal material came out much higher because when you are dividing in total weight it's much less. It wasn't inhibited, because production rates per unit surface area are routinely about the same. It wasn't that the material was too deep, it was not a shade-acclimated type thallus. The subtidal material was just a meter below mean lower low water in a very cleanwater area on San Clemented Island that doesn't get much light attenuation in the water.

HANSEN: From your collective results, if you were looking for the most highly productive strain of a particular species, I take it you would look for something with a very high surface/volume ratio first. What other characteristics: where would you collect it, etc.?

LITTLER: You would look for something that had a higher proportion of photosynthetic apparatus to general structural tissue. We do that by cutting sections and looking under fluorescent microscopes and scoring the amount of chlorophyll that fluoresces versus the amount of tissue that doesn't. You can do pigment extracts. The more pigmented it is, the more productive it would be, especially using low light intensity, but one has to worry about photoinhibition. Generally speaking, just the ratio of photosynthetic to structural apparatus should give you a very good predictor of an alga's productivity. Again it should have a high surface/volume ratio.

HANSEN: What about subtidal vs. intertidal?

LITTLER: There isn't any consistent relationship between subtidal and intertidal. The only relationship one might draw would be a tentative one. Since there is so much more stress in the intertidal, there might be more opportunistic species there. These opportunistic species are the ones that are high producers and fast growers.

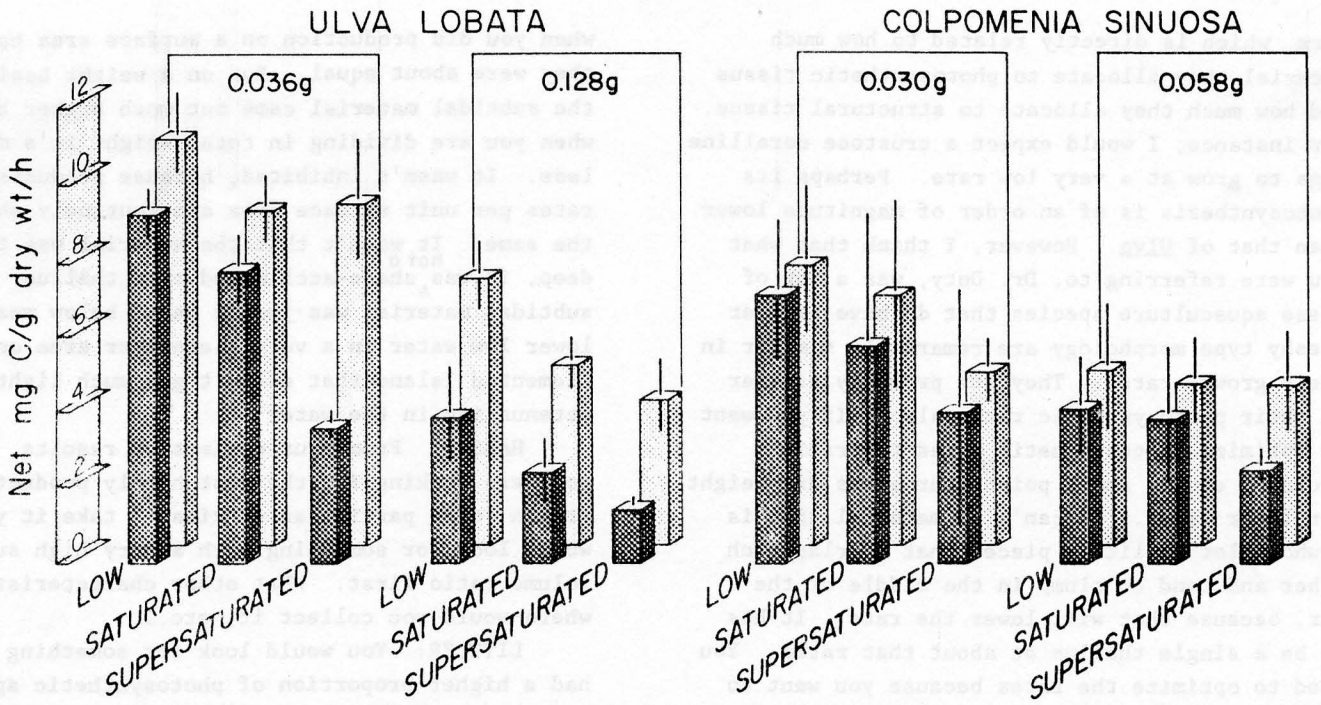

Figure 1. Apparent photosynthesis per gram dry weight of Ulva lobata and Colpomenia sinuosa as a function of the interacting effects of bottle size, mean thallus weight, and initial dissolved O_2 tension (low, saturated, and supersaturated). The darker histograms are for the 310 ml bottles, the lighter histograms are for 1220 ml jars. ± 95% confidence intervals are given by the straight lines at the top of each histogram. (modified from Littler 1979).

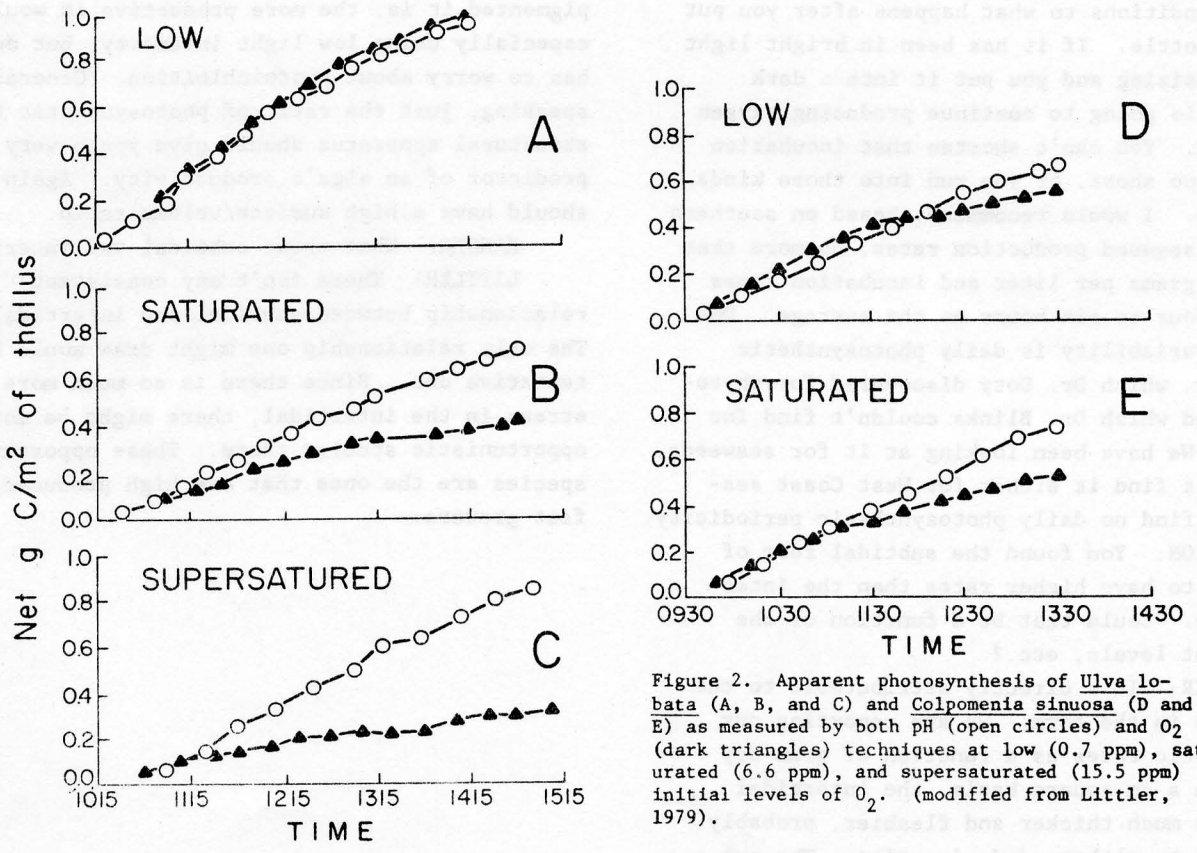

Figure 2. Apparent photosynthesis of Ulva lobata (A, B, and C) and Colpomenia sinuosa (D and E) as measured by both pH (open circles) and O_2 (dark triangles) techniques at low (0.7 ppm), saturated (6.6 ppm), and supersaturated (15.5 ppm) initial levels of O_2. (modified from Littler, 1979).

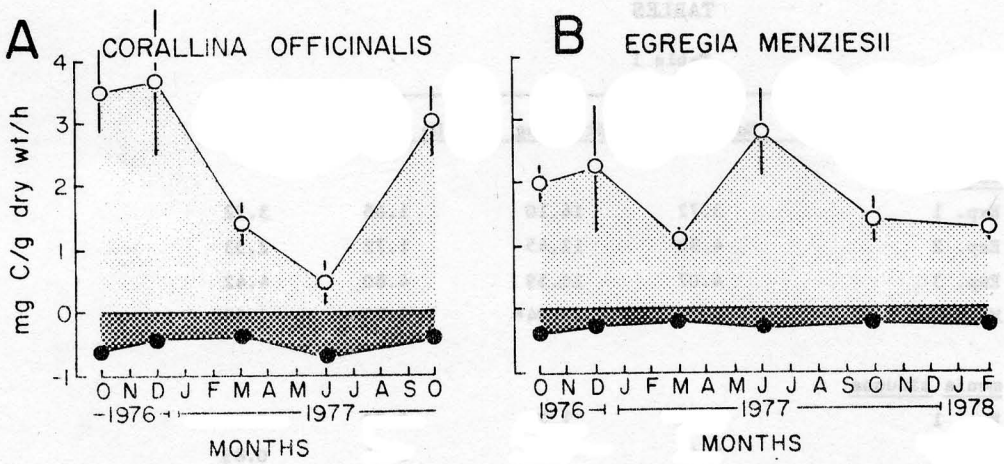

Figure 3. Seasonal net productivity (light) and respiration (dark) for Corallina (A) and Egregia (B). ± 95% confidence intervals are indicated by the straight lines bisecting each point. (modified from Littler and Arnold, 1979).

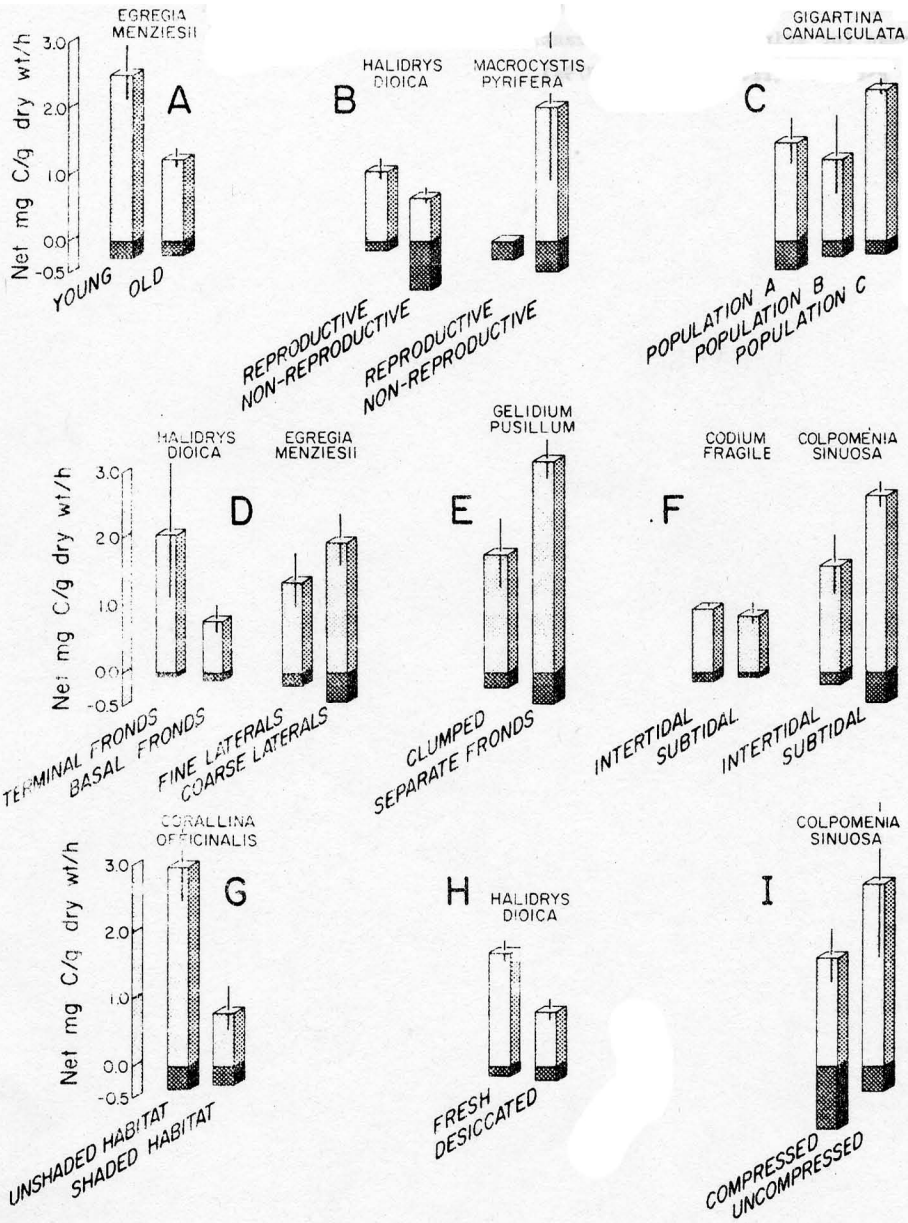

Figure 4. Net productivity and respiration for:

A: young vs. mature Egregia

B: reproductive vs. nonreproductive Halidrys and Macrocystis

C: wiry (populations a and b) vs. fleshy (population c) Gigartina

D: terminal vs. basal fronds of Halidrys and fine vs. coarse laterals of Egregia

E: clumped vs. separate thalli of Gelidium

F: intertidal vs. subtidal Codium and Colpomenia

G: Corallina from unshaded vs. shaded habitats

H: desiccated vs. fresh Halidrys

I: and compressed vs. uncompressed Colpomenia

(modified from Littler and Arnold, 1979).

TABLES

Table 1

Species and Experiment Number	Light		Dark	
	No Stirring	Stirring	No Stirring	Stirring
Ulva lobata				
Exp. 1	3.72	16.10	1.65	3.72
Exp. 2	4.80	12.45	1.72	2.53
Exp. 3	4.07	16.59	4.80	4.42
Means	4.20	15.04*	2.72	3.56
Colpomenia sinuosa				
Exp. 1	0.85	1.23	0.72	0.54
Exp. 2	1.40	1.36	1.11	0.89
Means	1.13	1.29	0.92	0.72

Slopes in mg C/g dry wt/h determined for regressions during continuous pH monitoring experiments of net photosynthesis and respiration. Asterisk indicates mean for stirring is significantly different from mean for no stirring at $P<0.05$. (from Littler, 1979a).