

SOURCES OF VARIABILITY IN MACROALGAL PRIMARY PRODUCTIVITY: SAMPLING AND INTERPRETATIVE PROBLEMS

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ABSTRACT

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Previous macroalgal production studies have been plagued by broad ranges of variability within experimental replicates that often exceed the seasonal or other parameters under investigation. As a first step toward understanding the factors responsible, eight rocky intertidal and subtidal macroalgae were examined for intrinsic sources of variation in photosynthetic performance and respiration relative to season, age, thallus part, reproductive state, external morphology, crowding, macrohabitat, microhabitat, desiccation, and physical injury. *Corallina officinalis* L. var. *chilensis* (Decaisne) Kützinger and *Egregia menziesii* (Turn.) Areschoug showed different seasonal production patterns with the minimum for *Corallina* and the maximum for *Egregia* occurring in the summer. The productivity of juvenile *E. menziesii* was 2.5 times higher than in structurally-differentiated mature individuals. *Halidrys dioica* Gardner had 2.8 times greater productivity in terminal vegetative branches than in basal fronds, while mature branches of *E. menziesii* were only half as productive as the young less-differentiated branches, indicating that as fronds mature, photosynthesis per unit of weight is effectively lowered as a result of increases in structural components. If the values for the least and most active thallus parts were used separately in production calculations, discrepancies of 250% for *Halidrys* and 130% for *Egregia* would be the result. The fertile terminal branches of *H. dioica* produced at a higher rate than either the basal fronds or vegetative terminal branches. Conversely, sporophylls of *Macrocystis pyrifera* (L.) C. Agardh showed no measurable net photosynthesis while vegetative blades fixed $2.01 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$. Respiration rates in fertile blades of both *H. dioica* and *M. pyrifera* were significantly lower than in vegetative fronds. More robust and highly-branched thalli of *Gigartina canaliculata* Harvey showed significantly ($P < 0.05$) greater photosynthetic rates than did the tougher more wiry individuals. The clumped form of *Gelidium pusillum* (Stackhouse) Le Jolis produced and respired at only half the rate of separate individuals. Subtidal populations of *Colpomenia sinuosa* (Roth) Derbès & Solier had both higher net production and respiration rates than intertidal thalli, while subtidal and intertidal *Codium fragile* (Sur.) Hariot did not show such differences. In *Colpomenia*, the intertidal form was thicker and heavier per unit area, resulting in self-shading that reduced the weight-based production. The shade-acclimated populations of *Corallina officinalis* var. *chilensis* showed much lower photosynthetic performances in full sunlight than did thalli acclimated to direct insolation. We found that desiccation significantly reduced net productivity in the lower intertidal species *H. dioica*. Physical damage reduced the photosynthetic performance of *C. sinuosa* by one-half while nearly

doubling its respiration. An understanding of variations such as those documented by this study is necessary for accurate analyses of macroalgal energetics and for the development of predictive insights into evolutionary strategies of carbon allocation. Therefore, much of the previous research on marine macroalgal productivity should be re-assessed in view of difficulties arising from environmental and intrinsic sources of metabolic variation.

INTRODUCTION

Much of the previous research on marine macroalgal primary productivity has been carried out without adequate consideration of methodological problems due to (1) incubation techniques, (2) environmental differences, and (3) intrinsic aspects of variability. Littler (1979) dealt with the first of these and made specific recommendations concerning macroalgal photosynthetic measurements in relation to initial oxygen levels, weight to incubation volume ratios, duration of incubation, and degree of mixing.

An earlier study (Littler et al., 1979) found that the large variability occurring within replicated experiments often overshadowed seasonal patterns of productivity even though considerable effort was made to optimize sample weight, incubation volume and time, mixing rate, and the initial dissolved oxygen level. Therefore, we found it necessary to examine those factors responsible for the major portion of this "within season" variability in photosynthetic performance. Such phenomena are equally problematical for both laboratory (e.g., Littler, 1973; Mathieson and Norall, 1975) and field studies (e.g., Johnston, 1969; Buesa, 1977) and, consequently, many of the published measurements and interpretations should be re-assessed in light of the difficulties arising from natural sources of metabolic variation. An understanding of the diverse sources and ranges of metabolic responses is central to (1) accurate estimates of individual macroalgal production rates, (2) analyses of the role of seaweed communities in marine productivity, and (3) construction of annual carbon budgets for use in analyzing the evolution of macroalgal production strategies.

Specifically, we examined the effects of 10 phenomena (including season, age, reproductive condition, external morphology, thallus portion, crowding, macrohabitat, microhabitat, desiccation, and physical stress) on photosynthetic and respiratory performances using the predominant macroalgae from a single rocky coastal system. We intentionally selected only those macroalgal species predicted to exhibit pronounced responses to a particular parameter, so that the levels of variability could be clearly documented.

MATERIALS AND METHODS

An extensive experimental program, totalling 285 incubations over a 16-month period, was conducted on eight different species of intertidal and subtidal macroalgae to begin to assess the intrinsic levels and causes of respiratory and photosynthetic variation. These experiments were divided into three broad

categories to include components of (1) within-species variation, (2) habitat variation, and (3) environmentally-induced variation. All analyses were conducted at Wilson Cove, San Clemente Island, California except for a single set of measurements on *Gelidium pusillum* (Stackhouse) Le Jolis performed at Dana Point Marine Refuge, Orange County, California, both areas in Southern California.

Net primary productivity (synonymous with net photosynthesis in this paper) and respiration were determined using Beckman Field Lab O₂ Analyzers and electrodes with 1220-ml wide-mouth clamp-lid bottles as light and dark incubation containers. The bottles were cleaned in aqua regia and aged for 30 days in distilled water prior to use. Dark bottles, produced by wrapping bottles with two layers of taped, heavy-duty aluminum foil, were incubated separately to prevent reflected light from impinging upon the light and blank bottles.

Several whole thalli were collected while submerged and placed in trays of ambient seawater. Thalli were then gently cleaned of obvious epiphytes and those that were heavily overgrown were discarded. Generally, whole organisms were incubated separately for the smaller species [*Codium fragile* (Sur.) Hariot, *Colpomenia sinuosa* (Roth) Derbès & Solier, *Corallina officinalis* var. *chilensis* (Decaisne) Kützinger, *Gigartina canaliculata* Harvey, and *Gelidium pusillum*]; the use of multiple small blades or branches was avoided to prevent self-shading. Incubations of the larger kelps [*Egregia menziesii* (Turn.) Areschoug, *Halidrys dioica* Gardner, *Macrocystis pyrifera* (L.) C. Agardh] were conducted on specific blades or branches as described below.

Seasonal variations in net productivity were examined from October 1976 to October 1977 for two of the predominant producers on San Clemente Island. Whole thalli of *Corallina officinalis* var. *chilensis* were collected on a seasonal basis from the same populations at a tidal height of +0.3 m, in reference to mean lower low water, and incubated separately. For *Egregia menziesii*, samples were taken from the same populations (−1.0 m) during all seasons (October 1976–February 1978). Segments (3 cm long) from the upper third of mature thalli with fine filiform laterals were used consistently.

To examine the effects of age on productivity, mature *Egregia* was sampled as above. Young undifferentiated *Egregia* plants (15 cm in length) were collected (February 1978) near the canopies of mature individuals and incubated whole.

Differences in photosynthesis and respiration due to reproductive state were assessed (February 1978) for *Halidrys dioica* and *Macrocystis pyrifera* collected at depths of −0.5 m and −5.0 m, respectively. The entire, non-reproductive basal fronds of *H. dioica* were incubated while only the upper half of reproductive fronds were used. Whole reproductive sporophylls and vegetative blades were assessed from mature *M. pyrifera* taken at similar depths (−5.0 m).

Variations between morphologically different populations were examined during June 1977 by sampling *Gigartina canaliculata* from three isolated

locations 15 m from each other at the same tidal height (+0.3 m). Individuals from one population (C) were less wiry, much more robust, and highly branched. The substratum type, degree of wave activity, and sun exposure appeared to be similar in all three cases.

Two large brown algae were examined for net productivity and respiration disparities among the differentiated thallus parts. *Egregia menziesii* was collected (October 1977) from a depth of -1.0 m, and 3-cm sections from the upper third of the thalli (containing fine filiform laterals) were compared with broad blade-like laterals taken from the basal portions of the same plants. Large, mature non-reproductive fronds of *Halidrys dioica* were collected (June 1977) from -0.5 m and the upper and lower portions were incubated separately.

To test the effects of crowding, naturally-occurring dense assemblages of *Gelidium pusillum* were collected (October 1977) from Dana Point at +0.5 m. Comparable quantities of whole tightly-packed clumps of thalli and dispersed individuals were incubated separately.

Macrohabitat-related dissimilarities were measured during June 1977 by sampling *Codium fragile* from intertidal (+0.2 m) and subtidal (-2.0 m) populations. Only the terminal portions, consisting of several dichotomies, could be incubated since the older portions were heavily overgrown with epiphytes. *Colpomenia sinuosa* was also collected from intertidal (+0.5 m) and subtidal (-2.5 m) populations. These specimens exhibited pronounced differences in the thickness of individual thalli; i.e., intertidal plants consistently had a much greater weight per unit area (12.5 mg cm^{-2}) compared to subtidal individuals (4.6 mg cm^{-2}).

For the microhabitat analyses, sun-acclimated plants of *Corallina officinalis* var. *chilensis* were collected (October 1977) at a tidal height of +0.3 m from a flat rock bench that was exposed to full sunlight throughout the day. Shade-acclimated thalli, with noticeably darker pigmentation, were collected from a deep crevice between boulders in an adjacent area at the same tidal height.

Desiccation stress was examined (October 1977) by drying whole, basal non-reproductive blades of *Halidrys dioica* from -0.5 m for 1.0 h (to an average of 60% of their fresh weight) on exposed bare rocks in the upper intertidal and comparing them with an otherwise similar set of non-desiccated plants.

The effects of compression, simulating physical damage, were assessed (in October 1977) for intertidal (+0.5 m) populations of *Colpomenia sinuosa*. Compression consisted of gently squeezing half of the samples twice by hand prior to incubation; comparisons were made with uncompressed individuals.

After sorting and cleaning, all thalli were carefully transferred to bottles completely filled with filtered ($10 \mu\text{m}$) seawater. Because the ambient seawater was supersaturated with O_2 , we poured 25-l batches from one contaminant-free bucket to another until a stock medium at air saturation was obtained. Several bottles were used to determine the initial dissolved O_2 for each incubation period.

Throughout the experiments, the thallus dry weights in the light bottles averaged 0.37 g l^{-1} with 0.46 g l^{-1} used for the dark bottles. A minimum of four light and two dark bottles for each experiment was incubated in clear polycarbonate trays between the starting times of 09.30 and 11.00 h and finishing times of 12.30 and 15.00 h with an average time span of 3.5 h. In the case of the larger kelps, incubation times were less (i.e. 2.5 h) since the representative thallus portions used were much larger than those for smaller less productive thalli. All bottles were thoroughly mixed at 15-min intervals to disrupt metabolically-induced diffusion gradients. Cooling was maintained by replenishing ambient seawater at 10–15-min intervals while the trays were placed in full sunlight near the water's edge. Temperature, light intensity (klux), and quantum flux ($\mu\text{E m}^{-2} \text{ s}^{-1}$, Ph.A.R.), measured with a Lambda Instruments L.I. 185 Quantum/Photometer, were monitored at 15–30-min intervals throughout each experiment (Table I).

At the end of each incubation period, the O_2 contents of the bottles were determined and compared with their initial levels. Each bottle contained a perforated acrylic partition to separate the thalli from the magnetic stir bar; each tray contained four bottles placed upon specially constructed four-unit stir motors that were air-driven by a foot pump from an inflatable boat kit. After the O_2 levels were recorded, thalli were blotted, placed in labeled polyethylene bags, and returned to the laboratory. The specimens were then dried at 80°C until they reached constant weight. In the case of *Corallina*, organic dry weight following 5.0 h of combustion at 500°C was used.

All O_2 values were converted to $\text{mg C fixed g dry wt.}^{-1} \text{ h}^{-1}$ by standard methods (Strickland, 1960), assuming a photosynthetic quotient of 1.00 which gives data that easily convert for comparisons with other studies where different *PQ* values were assumed. Oxygen levels in the light and dark blanks remained constant, so blank corrections were unnecessary.

TABLE I

Physical data [means \pm standard deviations (S.D.) and ranges] for San Clemente Island and Dana Point production studies

Location and date	Quantum flux [$\mu\text{E m}^{-2} \text{ s}^{-1}$ (Ph.A.R.)]			Intensity (klux)			Temp. ($^{\circ}\text{C}$)
	Mean	S.D.	Range	Mean	S.D.	Range	
San Clemente Island							
Oct. 1976	1130	275	370—1700	58	14	20—85	21.5
Dec. 1976	787	268	265—1150	38	15	7—65	16.5
March 1977	1494	270	800—1900	76	14	42—91	15.5
June 1977	1522	543	700—2400	82	30	40—130	18.0
Oct. 1977	1310	317	390—1700	62	13	21—76	20.5
Feb. 1978	1345	72	1200—1450	71	3	64—77	15.0
Dana Point							
Oct. 1977	>1200			>65			17.6

RESULTS

Organismic components of variation

Substantially different seasonal patterns in net primary productivity were evident for *Corallina officinalis* var. *chilensis* (Fig. 1a) and *Egregia menziesii* (Fig. 1b). In *Corallina*, highest values occurred during October and December. March rates were significantly lower ($P < 0.05$) with lowest rates in June being only 13.6% of the highest values throughout the study. The 95% confidence limits were broad, averaging $\pm 33\%$ of the mean net primary production. Respiration averaged $0.38 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$ and remained relatively constant. *Egregia* (Fig. 1b) also exhibited marked seasonal fluctuations with a low in March that was only 40% of the highest rate. Variation, as reflected by the 95% confidence intervals, averaged $\pm 25\%$ of the seasonal means. As was the case with *Corallina*, respiration showed little seasonal difference (mean of $0.23 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$).

Whole young thalli of *Egregia menziesii* (Fig. 2a) fixed $1.00 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$, a value 2.5 times that of fully-differentiated mature thalli (significantly different at $P < 0.05$). Respiration was not different ($P > 0.05$) between the blades of young and old individuals of this species.

Significant differences ($P < 0.05$) were noted between fertile and non-fertile portions of *Halidrys dioica* and *Macrocystis pyrifera* (Fig. 2a); however, the trends were opposite. Reproductive blades of *H. dioica* produced at the rate of $1.07 \text{ net mg C g dry wt.}^{-1} \text{ h}^{-1}$, a value 1.6 times that of vegetative material; whereas the respiration of fertile blades ($0.15 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$) was only one-fifth that of non-reproductive thalli ($0.72 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$). Conversely, reproductive sporophylls of *M. pyrifera* showed no measurable net productivity (Fig. 2b) while vegetative blades produced $2.01 \text{ net mg C g dry wt.}^{-1} \text{ h}^{-1}$. Respiration was statistically lower ($P < 0.05$) in the sporogenous tissue of *M. pyrifera* (0.31 vs. $0.44 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$).

The highly branched and fleshy thalli of *Gigartina canaliculata* (population C in Fig. 2c) produced at a rate 1.8 times higher than that of two less branched and more wiry populations of the same species taken from different locations on the shore. Respiration averaged $0.33 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$ and differences were non-significant ($P > 0.05$) among the three populations.

The terminal fronds of *Halidrys dioica* were 2.8 times more productive ($2.07 \text{ net mg C fixed g dry wt.}^{-1} \text{ h}^{-1}$) than were basal fronds of the same organism ($P < 0.05$, Fig. 2d). Respiration for terminal fronds was different ($P < 0.05$) from that of basal fronds (mean respiration = $0.88 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$). The fine filiform segments of *Egregia menziesii* were only 68% as productive as the coarse thalli (1.34 vs. $1.98 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$). Respiration was significantly higher (2.5 times greater, Fig. 2d) for the latter than for the former.

The naturally-clumped aggregated form of *Gelidium pusillum* produced at slightly over half the rate ($P < 0.05$) of non-crowded fronds (1.80 vs. 3.23).

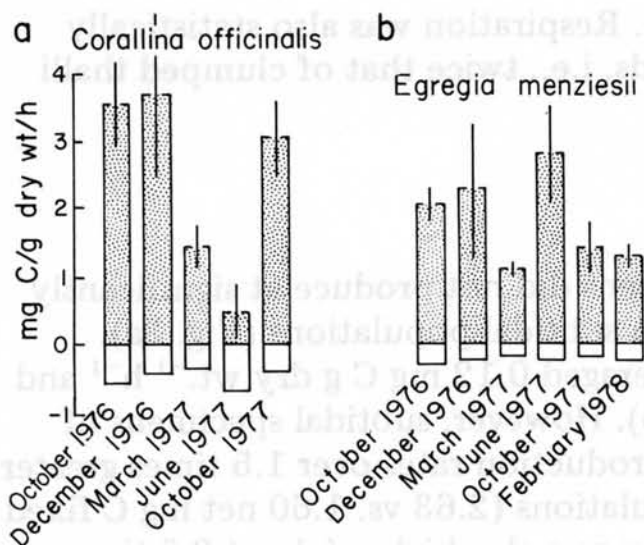


Fig. 1. Seasonal net productivity (dark) and respiration (light) for *Corallina* (a) and *Egregia* (b). $\pm 95\%$ confidence intervals are indicated by the straight lines at the top of each histogram.

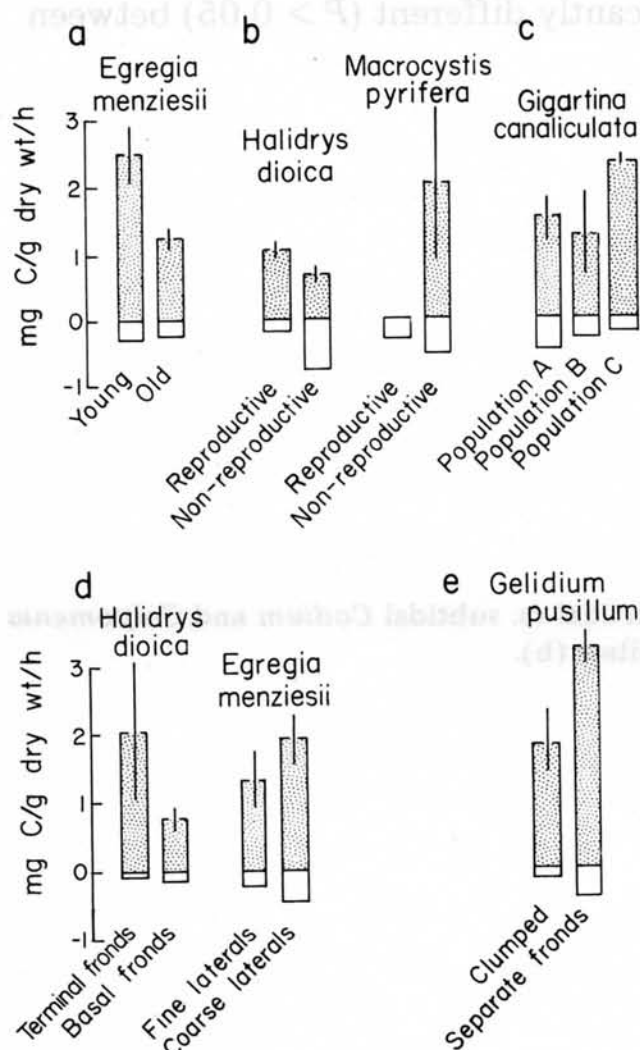


Fig. 2. Net productivity and respiration for young vs. mature *Egregia* (a), reproductive vs. non-reproductive *Halidrys* and *Macrocystis* (b), wiry (populations A and B) vs. fleshy (population C) *Gigartina* (c), terminal vs. basal fronds of *Halidrys* and fine vs. coarse laterals of *Egregia* (d), and clumped vs. separate thalli of *Gelidium* (e).

net mg C fixed g dry wt.⁻¹ h⁻¹, Fig. 2e). Respiration was also statistically higher ($P < 0.05$) in the separated fronds, i.e., twice that of clumped thalli (Fig. 2e).

Habitat components of variation

For *Codium fragile*, intertidal specimens did not produce at significantly greater rates ($P > 0.05$) than those from subtidal populations (Fig. 3a). Respiration for the two populations averaged 0.12 mg C g dry wt.⁻¹ h⁻¹ and was not statistically different ($P > 0.05$). However, subtidal specimens of *Colpomenia sinuosa* (Fig. 3a) showed production rates over 1.5 times greater ($P < 0.05$) than those of intertidal populations (2.63 vs. 1.60 net mg C fixed g dry wt.⁻¹ h⁻¹, respectively); respiration was also higher (about 2.5 times greater, $P < 0.05$) in the subtidal samples (0.48 vs. 0.19 mg C g dry wt.⁻¹ h⁻¹).

Corallina officinalis var. *chilensis* from an unshaded habitat (Fig. 3b) had nearly four times the productivity ($P < 0.05$) of the same species from a shaded habitat (3.03 vs. 0.80 mg C fixed g dry wt.⁻¹ h⁻¹). Mean respiration was 0.33 mg C g dry wt.⁻¹ h⁻¹ and was not significantly different ($P > 0.05$) between the two populations.

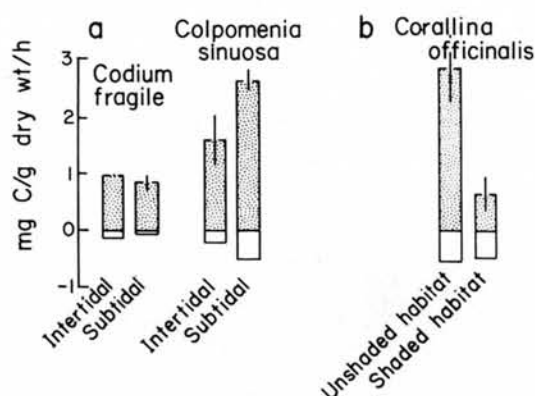


Fig. 3. Net productivity and respiration for intertidal vs. subtidal *Codium* and *Colpomenia* (a) and *Corallina* from unshaded vs. shaded habitats (b).

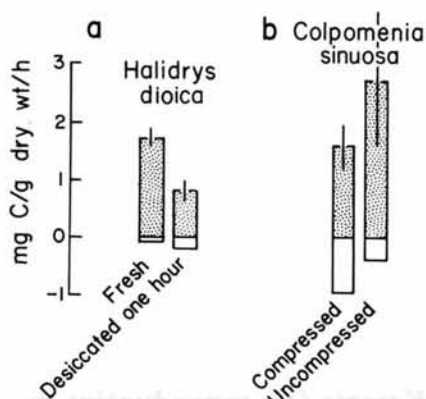


Fig. 4. Net productivity and respiration for desiccated vs. fresh *Halidrys* (a) and compressed vs. uncompressed *Colpomenia* (b).

Environmental components of variation

Fresh thalli of *Halidrys dioica* (Fig. 4a) had double the net productivity of thalli dried for 1 h, i.e., $1.71 \text{ mg C fixed g dry wt.}^{-1} \text{ h}^{-1}$ for fresh thalli vs. 0.84 for desiccated thalli. Respiration was not significantly different ($P > 0.05$) after the desiccation period in this alga (mean value of $0.16 \text{ mg C g dry wt.}^{-1} \text{ h}^{-1}$).

The physical compression of *Colpomenia sinuosa* (Fig. 4b) reduced the net photosynthetic rate to almost half that of unstressed thalli (1.68 vs. $2.80 \text{ mg C fixed g dry wt.}^{-1} \text{ h}^{-1}$) while it caused respiration to nearly double; both changes were statistically different at the $P < 0.05$ level.

DISCUSSION AND CONCLUSIONS

Seasonality

Numerous laboratory studies have documented seasonality of primary productivity in marine macroalgae; however, few common patterns have emerged. For example, Zavodnik (1973) found gross production rates in the laboratory to be highest in summer and lowest in winter for *Fucus virsoides* (Don) J.

Agardh, while field data showed opposite trends. Others (King and Schramm, 1976a; Brinkhuis, 1977) reported a tendency for many marine macroalgae to have highest rates of light-saturated photosynthesis in spring and summer corresponding to seasonal growth patterns. Alternatively, Hata and Yokohama (1976) recorded highest rates of photosynthesis in four out of seven species during winter, irrespective of experimental temperatures. In the present study, both *Corallina officinalis* var. *chilensis* and *Egregia menziesii* showed opposite seasonal patterns (Fig. 1a and b) with the photosynthetic minimum for the former and the maximum for the latter occurring in summer.

Factors that control seasonality of net primary production in the field are poorly understood for most intertidal macroalgae. Littler et al. (1979) examined the seasonal patterns of net daily photosynthesis and standing stock for the 13 predominant intertidal algae on San Clemente Island, California. Highest rates of net production were recorded in summer for nine of the species, with minimum rates in the spring and to a lesser extent during winter. As in the present study, seasonal patterns of production were also found to be highly variable although there was a tendency for most species to attain peak daily photosynthetic rates concurrent with higher temperatures and longer day lengths.

Age and thallus parts

Growth and development in benthic macroalgae is multifarious, ranging from relatively undifferentiated forms with diffuse growth, such as *Ulva* sp., to the massive and structurally complex thalli of kelps (Laminariales) which

have specialized meristematic tissue. In all members of the Laminariales, the young sporophyte consists of a simple elongated polystromatic blade. At this stage there is very little structural differentiation (Littler and Littler, 1980) and a high ratio of photosynthetic to non-photosynthetic tissue. Therefore, young sporophytes were expected to have greater weight-based photosynthetic rates than mature thalli. Our experiments with *Egregia menziesii* (Fig. 2a), where the productivity of whole young plants was 2.5 times greater than blade portions of fully-differentiated mature thalli, clearly substantiated this prediction. Respiration rates, although slightly higher, were not significantly different ($P > 0.05$) in the younger undifferentiated plants.

Most studies on the effects of age relative to physiological performance have been concerned with ontogenetic gradients within mature thalli or isolated lamina. Both King and Schramm (1976b) and Brinkhuis (1977) recorded highest photosynthetic rates in the terminal growing tips of mature *Fucus vesiculosus* L.; Küppers and Kremer (1978) noted similar patterns for both light and dark $^{14}\text{CO}_2$ -fixation in three species of *Fucus* (including *F. vesiculosus*). Similarly, for *Halidrys dioica* (Fig. 2d), also a fucoid species, we found considerably higher productivity (2.8 times) in terminal vs. basal fronds even though respiration was not significantly different.

The mature branches of *Egregia menziesii* (Fig. 2d) containing fine filiform laterals were not as productive (50%) as the less differentiated young branches, but respiration was much greater (double) in the latter. This suggests that as branches mature and become differentiated, photosynthesis per unit of weight is lowered due to allocation of materials to structural components. Chapman (1962), in a related study, found a photosynthetic gradient within each flattened juvenile branch of *Egregia*; the tips showed higher photosynthetic rates per unit weight than the basal portions, with the opposite relationship occurring when the rates were calculated for area. This difference was attributed (Chapman, 1962) to the greater thickness per unit surface area near the base of the fronds. Also, single blades of *Macrocystis pyrifera* (Clendenning, 1971) and *Laminaria digitata* (Hud.) Lamour. (King and Schramm, 1976b; Küppers and Kremer, 1978) showed steeply rising photosynthetic rates with increasing distance from the base.

Therefore, physiological and biochemical gradients that occur within the blades of laminarialean species must be carefully considered in productivity studies. For example, if the photosynthetic data on different thallus portions of *Halidrys* and *Egregia* were extrapolated to whole plant or community productivity, the discrepancies between the least and most active parts could be as high as 250 and 130%, respectively. Also, the inconsistent measurement of different portions of structurally-complex species during seasonal studies can effectively mask the actual patterns.

Reproduction

Profound biochemical and physiological changes occur within reproductive thalli prior to the onset of gamete or spore release. Manometric measure-

ments of photosynthesis and respiration on *Ulva lactuca* L. (Haxo and Clendenning, 1953) showed that the reproductive margins exhibit respiration rates two to four times higher than the corresponding vegetative tissue. Net photosynthesis was also found to be reduced by 50 to 66% in reproductive thalli. We found (Fig. 2b) contrasting responses of photosynthesis and respiration as a function of reproductive state in *Halidrys dioica* and *Macrocystis pyrifera*. In the case of *Halidrys*, the fertile tissue is located at the terminal ends (receptacles) of mature blades which, even when non-reproductive, had higher net productivity compared to the lower basal blades (Fig. 2d); however, when reproductively mature, these tissues showed still higher rates (Fig. 2b). Related to this is the finding (McLachlan and Bidwell, 1978) that eggs and sperm are photosynthetically competent in the closely-related *Fucus serratus* L.; other studies on *F. serratus* (Kremer, 1975) similarly showed that photosynthesis was highest in regions of reproduction and new growth. Another pertinent study (Lobban, 1978) on translocation of ^{14}C in *Macrocystis pyrifera*, suggests that sporophylls function as sink blades, receiving photosynthate from more photosynthetically-active source blades and, hence, it is not surprising that our data showed net photosynthesis to be overshadowed by respiration.

Morphology

The range of morphological forms within an algal species is often quite large (Peterson, 1972; Cheney and Babbel, 1978; Clayton, 1978). Neither the factors that regulate morphological plasticity nor the physiological and biochemical changes associated with different growth forms are clearly understood for marine benthic algae. In the case of *Caulerpa racemosa* (Forsskål) J. Agardh (Peterson, 1972), specimens developing under low light intensity tended to be more flattened and have higher surface area to volume ratios, reduced light compensation intensities, larger gross photosynthesis/respiration ratios, and higher net photosynthesis at lower light intensities than high-light forms.

All three of the *Gigartina canaliculata* populations that we studied occupied subjectively similar habitats; i.e., no obvious differences in substrate, wave exposure, or light regime were noticed. However, the fleshy and more highly-branched growth form (population C, Fig. 2c) had significantly greater photosynthetic rates than the less branched and more wiry populations (A and B, Fig. 2c). The tougher wiry populations contained proportionately more non-photosynthetic structural tissue which concomitantly reduced the overall photosynthetic performance per unit of weight. However, the respiration rates of the three populations did not differ significantly ($P > 0.05$). Evidence of physiological heterogeneity correlated with morphological form, as obtained in the present study and by Peterson (1972), is crucial to understanding the adaptive significance of these interpopulational variations. Additionally, this kind of information can be quite useful in elucidating taxonomic problems within morphologically diverse species (e.g., Wynne and Norris, 1976).

Crowding

Clumping of thalli may increase intraspecific competition for light and nutrients while rendering advantages such as environmental tolerance (Hay, 1978). In a related study, Dawes et al. (1978) attributed the low photosynthetic rates in *Cladophora* (monitored in air after desiccation as well as submerged) to its clumped habit directly on the mud/water interface, a growth form that they felt consequently ameliorates its exposure to air, thereby, increasing its resistance to desiccation. During the present study, the clumped form of *Gelidium pusillum* photosynthesized at approximately half the rate of separated fronds (Fig. 2e); respiration was also higher in the individual thalli (about double that of clumped fronds). Also, during the investigation of Littler (1979), fewer macroalgal individuals in small bottles consistently outperformed the more numerous thalli of the same species in large jars even though the lower weight/volume ratios should predictably have resulted in higher production rates in the jars. This was attributed to competition for CO₂ and the mutual self-shading by overlapping thalli even when surrounded by relatively large volumes of seawater.

Habitat

Distinct metabolic differences were shown between subtidal and intertidal populations in one case but not the other (Fig. 3a). Subtidal populations of *Colpomenia sinuosa* had both higher net production and respiration rates than intertidal populations; whereas, for *Codium fragile*, production rates between intertidal and subtidal populations were similar. *Ascophyllum nodosum* (L.) Le Jolis and *Fucus vesiculosus*, acclimated at a depth of 4 m (Ramus et al., 1977), had higher photosynthetic rates than the same plants acclimated to surface light conditions, due in part to higher concentrations of antenna pigments. Similar phenomena could partly account for the differences in subtidal and intertidal populations of *Colpomenia* examined in the present study; however, morphological differences are also important. For example, the intertidal thalli of *Colpomenia* had a noticeably greater weight per unit area (12.5 mg cm⁻²) as compared to subtidal plants (4.6 mg cm⁻²). Consequently, intertidal thalli with comparable photosynthetic area (tissue) showed lower net production rates on a weight basis because of the additional self-shaded tissue. Related to this observation, Colombo and Orsenigo (1977) noticed that *Halimeda tuna* (Ellis & Solander) Lamour. from deep water (-6.0 m) had thinner segments, larger utricles, and thinner cell walls than the same species sampled from shallow (-0.5 m) populations. Although the increase in structural tissue of intertidal populations reduced the weight-based production, such morphological responses appear to be adaptive by conferring greater resistance to desiccation and physical stress (Littler and Littler, 1980).

The lack of photosynthetic differences per unit weight for subtidal and intertidal thalli of *Codium fragile* (Fig. 3a) contrasts somewhat to the results

produced by Ramus (1978), where thalli suspended subtidally for 7 days at low light intensity had much greater (1.9 times) area-based photosynthesis at surface light intensities than fronds taken from the surface. However, when our data were normalized to surface area, subtidal *Codium* also showed significantly ($P < 0.05$) greater productivity (1.2 times) than intertidal populations.

Intertidal populations of *Corallina officinalis* var. *chilensis* collected from "sun" and "shade" microhabitats also showed marked differences in net production (Fig. 3b); i.e., sun forms were 3.8 times more productive than shade populations. Both Littler (1973) and Peterson (1972) have also shown photoinhibition to be common when shade-acclimated algae are exposed to full sunlight (>100 klux).

Desiccation

Many field observations (see Schonbeck and Norton, 1978) have suggested the importance of desiccation in determining the upper limits of intertidal macroalgae. However, the effects of water loss on photosynthesis and respiration have not been uniform for all species examined and are most closely correlated with habitat differences. For example, Mathieson and Burns (1971) reported that intertidal *Gigartina stellata* (Stackhouse) Batters showed faster recovery of photosynthetic and respiratory capacity upon re-immersion than the deeper-growing *Chondrus crispus* Stackhouse. *Pelvetia canaliculata* (L.) Decaisne & Thuret, the species found highest on the shore by Schonbeck and Norton (1978), demonstrated the greatest ability to recover photosynthetic response following desiccation; this capacity was found to be progressively less in other fucoids inhabiting lower levels. We also noted that lower intertidal *Halidrys dioica* (a fucoid alga) showed significant reductions in net productivity after drying (Fig. 4a). Ogata and Matsui (1965), Chapman (1966), and Schonbeck and Norton (1978) have all demonstrated that water loss generally reduces net photosynthesis and respiration when measured on re-immersed thalli. Recent evidence (Wiltens et al., 1978) implicates the electron transport between photosystems I and II and water splitting (O_2 evolution) capability as the photosynthetic reactions most sensitive to desiccation.

Physical stress

Physical (compression) injury lowered the photosynthetic rate of *Colpomenia sinuosa* to almost half while nearly doubling respiration (Fig. 4b). The incubation of plant tissues cut into small discs or torn into small segments has been used routinely to measure the metabolic activity of seaweeds. However, this can cause errors in the measurement of production, a phenomenon observed (UNESCO, 1973) to severely affect respiration in the brown alga *Padina* sp. In addition, Hatcher (1977) noticed that in freshly-cut segments of *Laminaria longicruris* De la Pylaie, even after 12 h of acclimation, respiratory

rates were 1.80 times that of whole plants; a second effect of cutting was to dramatically increase the variability among replicates for both respiration and photosynthesis. A partial explanation for this lies in the fact that the tissues of many Phaeophyta contain high concentrations of phenolic compounds (Ragan and Jensen, 1977) and when wounded (Sieburth, 1968) or severed (Dromgoole, 1978), these are released from the cells into the surrounding seawater. The phenolic compounds then become rapidly oxidized to their corresponding quinones and, thus, when exuded in sufficient quantity, obscure photosynthetic and respiratory exchange of oxygen.

In conclusion, depending on the objectives and questions being asked, the kinds and ranges of variability documented here, as well as those pointed out by Littler (1979), must be taken into account when designing studies on marine macroalgal metabolism. This is equally critical for both field and laboratory studies and much of the published research should be re-assessed in light of the differences demonstrated. In addition, intrinsic populational variations must be known before the contributions of benthic algae to marine productivity can be accurately estimated. This becomes particularly crucial when calculating annual carbon budgets (Hatcher et al., 1977; Johnston et al., 1977) or constructing mathematical production simulation models (Belyaev et al., 1977). Also, the diverse sources and levels of metabolic responses are related to evolutionary strategies that must be understood before predictive theories will be forthcoming concerning the important selective processes that have molded macroalgal production patterns. Littler and Littler (in press) have taken an initial approach by showing that a number of hypothetically-adaptive production, morphological, and ecological strategies have been selected in various species of macroalgae.

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