**Philippine Journal of Science**
151 (S1): 207-221, Marine Botany
ISSN 0031 - 7683
Date Received: 03 Aug 2021

# Linking Thallus Morphology with P-I Curves of 50 Macrobenthic Algae from Bolinao, Pangasinan, Philippines

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**This study demonstrated that thallus morphology could affect a species' capacity to utilize light for photosynthesis and, hence, will affect its productivity. Fifty (50) macroalgal species collected from an intertidal habitat in Bolinao, Pangasinan, Philippines were grouped into five "functional-forms" based on their inferred productivity: functional-form group (FFG) A: very thin tubes/sheets/strips, FFG B: thin sheets/delicately branched, FFG C: medium-thick blade/coarsely branched with dense ramuli, FFG D: heavily thick branches/segments or with moderate calcification, and FFG E: heavily calcified. Their photosynthesis-irradiance (P-I) curves were determined through the measurement of oxygen evolved in a closed system after 1-h incubation under six different light treatments. P-I curve parameters such as $P^n_{max}$, $I_k$, $I_c$, $\alpha$, and $R_d$ were assessed to determine the groups' physiological responses to light. The thickness of thallus blades, coarseness of branches, complex branching, and calcification appeared to lessen photosynthetic capacity, as shown by the significantly decreasing trend of $P^n_{max}$ from FFGs A–E. FFG A also showed the steepest slope (highest mean α value) compared with the rest of the functional-form groups, indicating their efficiency to utilize low light for photosynthesis. Light saturation and compensation values were less distinct in differentiating the functional form groups, probably because the seaweeds examined were all collected from the same shallow intertidal zone, suggesting their acclimation to similar photon flux densities. Results from this study fit the prediction of the function form hypothesis for seaweeds quite well.**

Keywords: compensation irradiance ($I_c$), initial slope (α), photosynthesis, saturating irradiance ($I_k$), thallus morphology, tropical seaweeds

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## INTRODUCTION

The Philippines, an archipelagic country with an extensive shoreline, is rich in seaweed resources (Trono 1999; Ganzon-Fortes 2012; Ang *et al*. 2013). However, studies dealing with their contribution to marine primary productivity are very limited, with most studies focused mainly on phytoplankton, seagrasses, and mangroves. Macroalgae are important components of coral reefs and contribute substantially to reef productivity [*e.g.* Hay (1997), Harborne *et al*. (2006)]. However, most local ecological studies on macroalgae deal mainly with their spatial distribution and abundance, biodiversity, and phenology (Trono and Saraya 1987; Largo and Ohno 1992; Ganzon-Fortes 2012; Baleta and Nalleb 2016).

Littler (1980), Littler and Littler (1980), and Littler and Arnold (1982) have demonstrated that morphological form and physiological function are intimately related in macroalgae. For example, macroalgal forms with a high surface area to volume ratio (*i.e.* in this case, the thin and delicately branched forms) have a higher photosynthetic capacity and have high productivity than forms with low ratios (*i.e.* in this case, the coarsely branched and highly calcified forms). This interrelationship is fitted into a hypothetical model – the "functional-form" model, which sorts macroalgal life-forms into several groups (Littler and Arnold 1982) (*e.g.* sheet-like, filamentous, coarsely branched, thick leathery, jointed calcareous, and crustose groups) and ranks the sheet forms having the highest surface area to volume ratio as the most productive, whereas the encrusting ones as the least. Exceptions to the functional-form pattern exist, *e.g.* in clumped forms of some filamentous algae that resulted in self-shading. Nonetheless, the model provides a promising tool for interpreting co-evolved interrelationships between algal physiology and morphology (Littler and Arnold 1982), specifically in predicting the outcome of productivity-related ecological processes without having to associate such interrelationship with species of a particular geographic region or phylogenetic line.

Due to its easy application and the reduced cost and workload when compared with studies that needed to deal with species-level identifications, the functional form model has found reasonably wide ecological applications. It provided insights into the estimation of photosynthesis and its photon flux density relationships in a microalgal turf assemblage (Williams and Carpenter 1990) and in the study of the structure of macroalgal communities on intertidal rocky shores (Steneck and Dethier 1994; Tobin *et al*. 1998). It made it easier to assess the response of complex subtidal algal communities to environmental disturbances at temporal and spatial scales (Lavorel *et al*. 1997), to follow the impact of environmental stress (Hay 1981; Balata *et al*. 2011), and to understand recolonization process of a degraded ecosystem (Ducrotoy and Pickaert 2001). The concept was further applied to evaluate the importance of substratum stability on algal growth (Littler and Littler 1984), algal resistance to herbivores (Littler and Littler 1980; Steneck and Watling 1982), algal responses to mechanical stress under various flow regimes (Norton *et al.* 1981), and strain selection in seaweed culture (Hanisak *et al.* 1990).

However, a detailed review of 49 studies that provided experimental tests of the functional form/group models indicated both the acceptance and rejection of the functional form hypothesis (Padilla and Allen 2000). Many of these studies found that primary productivity (photosynthesis and nutrient uptake) correlated well with algal morphology, whereas most studies addressing algal susceptibility to herbivores, tolerance to physiological stress, or functional ecology relative to successional stages (*e.g.* seaweed community progressing from young to mature) found little support of this hypothesis. Furthermore, when a different function is considered, a species might be assigned to different groups, making it more difficult to interpret the general applicability of the hypothesis.

The present study was conducted to test the applicability and practicality of the "functional-form hypothesis" in a tropical setting, *i.e.* the Philippines. As suggested by Padilla and Allen (2000), some success with the application of the functional-form group (FFG) model is found when groupings are based on a specific function and species are distributed to groups based on a functional criterion. In this study, we grouped 50 macroalgal species according to the "inferred function" (productivity) of their thallus forms. We used the photosynthesis irradiance curve (P-I curve) to verify our grouping. This physiological tool provided not only data on the species' maximum photosynthetic rate at light saturation ($P_{max}$) – as was done in most previous studies – but also data on the saturating irradiance of photosynthesis ($I_k$), irradiance at compensation point ($I_c$), light harvesting efficiency at limiting photon flux densities ($\alpha$, initial slope of the curve), and respiration in darkness ($R_d$) (Henley 1993). Results of this study provide essential baseline information on the photosynthetic response of tropical macroalgae to different levels of irradiance in the form of their P-I curves, as well as the application of this information to predict their patterns of primary productivity in the light of the functional form hypothesis.

## MATERIALS AND METHODS

### Collection Site

Seaweed materials were collected along the coast of Patar, Bolinao, Pangasinan, northern Philippines (16.34°N, 119.79°E). The site has a wide intertidal reef flat (about 114 m long) of calcareous bedrock overlain with a thin layer of fine to coarse sand. Shallow tidepools are common and cracks that deepened into crevices near the seaward margin receive breaking waves that create moderate to high water motion. Water is generally clear during calm conditions but could be slightly turbid during monsoon months (September–January). Depth is shallow, up to about 1 m during high tide, but deeper in tidepools near the shore (up to about 1.5 m) where seagrasses predominate on the sandy substratum. During low spring tides that occur during daytime (*e.g.* at 0700–1500 h), the upper littoral zone of the site is exposed to air for several hours, whereas the mid littoral zone is occasionally wetted by incoming waves.

### Collection and Preparation of Seaweed Samples

A total of 50 species were collected and used in experiments during the summer season of March–May 2006. Seaweed samples were carefully collected by hand and placed in labeled plastic bags containing a small amount of ambient seawater. This was to prevent desiccation as a possible intrinsic source of variation in photosynthetic performance (Littler and Arnold 1982). These samples were kept in a Coleman box filled with 2 cm deep ambient seawater to keep them moist and to maintain the temperature at ambient level (28 ± 2 °C) during the 45-min transport to the laboratory at the Bolinao Marine Station of the Marine Science Institute (MSI), College of Science (CS), University of the Philippines (UP). Upon arrival at the laboratory, samples were immediately sorted to species, cleaned of epiphytes and debris, and thoroughly washed with running seawater. For the preparation of test samples, whole thalli were used for small species (fresh weights = 1.5–2.5 g), whereas those with large thalli, blades, or branches were trimmed or cut (fresh weights = 0.709 ± 0.626 g). For those with very large thalli, only young parts were used in the experiments. Where possible, the use of multiple blades or branches was avoided to prevent self-shading during sun incubation. All test samples were placed in respective white plastic basins immersed in filtered ambient seawater and kept in the culture shelf maintained at 12L:12D photoperiod, 70–80 μmol photons $m^{-2}$ $s^{-1}$ irradiance, and 26 ± 2 °C room temperature for a maximum of 3 d after collection. Herbarium voucher specimens of these materials were also prepared and deposited in the G.T. Velasquez Phycological Herbarium of the MSI (Herbarium Code: MSI).

### Photosynthesis-Irradiance (P-I) Curve Determination

***Photosynthetic oxygen evolution measurement.*** The technique of measuring photosynthetic rates by oxygen evolution was based on the works of Dawes and Koch (1988) and Dawes (1989, 1992). To avoid diurnal periodicity of photosynthesis, photosynthetic measurements were done during 1000–1400 h (Ganzon-Fortes 1997) and respiration at 0800–0930 h. The method used could only accommodate two species per experimental run per day; thus, only six species were examined within the allowable 3-d laboratory holding period after each collection period.

There were six light treatments: 100, 65, 35, 24, 13, and 8% of natural irradiance (sunlight) were achieved using 0–5 layers of black nylon screen, respectively, wrapped around each corresponding white incubation basin. For 0% light (dark respiration), the incubation basin was of black plastic material wrapped with two layers of black garbage bag and kept inside a cabinet during incubation. Each incubation basin accommodated four 350-mL BOD bottles, each filled with ambient filtered seawater (27–28 °C, 32–33 psu, 8.3 pH). Three of these bottles contained previously weighed test samples of an experimental seaweed species (n = 3) prepared earlier (see previous section), and one bottle was without any seaweed to serve as the control for change in oxygen level due to plankton photosynthesis, as well as plankton and bacteria respiration (*i.e.* to be used to correct change in $O_2$ level from plankton photosynthesis and bacterial respiration). The BOD bottles were laid on their sides in the incubation basin immersed in tap freshwater that was regularly replaced every 15 min during solar incubation to keep the temperature in the bottles at ambient levels of 27–28 °C. Irradiance was recorded using a cosine (2 pi) collector sensor (LI-192, LI-COR) connected to a data logger (LI-1000, LI-COR). Full solar or 100% irradiance at the time of the experiments was 879–1203 μmol photons $m^{-2}$ $s^{-1}$ and 50–106 μmol photons $m^{-2}$ $s^{-1}$ when reduced to 8% (lowest light treatment). The incubation period per irradiance level was 1 h, before and after of which the dissolved oxygen (DO) content in each bottle was measured with a Clark-type oxygen electrode probe (YSI 5750) connected to a DO meter (YSI Model 58) while under continuous stirring on a magnetic stirring plate. After the experimental run, the dry weight of each of the 21 test samples (7 treatments x 3 replicates) of each experimental species was determined as follows: the mean dw:ww ratio of each species was first obtained using four randomly chosen test samples (n = 4) of the same species that had been dried to constant weight in an oven set at 65 °C. The dry weight of the rest of the test samples of the same species was then calculated by multiplying the

earlier recorded fresh weight (ww) of each test plant by this mean dw: ww ratio.

The net photosynthetic rate per irradiance level, Pn, was expressed in $mgO_2$ $gdw^{-1}$ $h^{-1}$ and computed using the formula:

$$P_n = \frac{(Final\ O_2 - Initial\ O_2\ per\ bottle\ \#1\ to\ 3) - (Final\ O_2 - Initial\ O_2\ of\ blank\ bottle\ \#4)}{Dry\ wt.(g)\ of\ test\ plant\ per\ bottle\ \#1\ to\ 3} h^{-1} \quad (1)$$

***P-I curve fitting.*** The net photosynthetic rates per irradiance level (n = 3) were curved-fitted with a non-linear least square regression comparing the differences between measured and calculated values using the Solver Module in Excel (Microsoft Corp., Redmond, USA) [as described by Roleda *et al*. (2006)], following an exponential equation model:

$$P_n = P_{g\ max}\ [1 - exp(-\alpha / P_{g\ max})(I)] - R_d \quad (2)$$

where $P^n$ is the net photosynthesis, $P^g_{max}$ is the gross photosynthesis, α is the initial slope of the curve, I is the incident irradiance, and $R_d$ is the dark respiration rate [Webb *et al*. 1974; Jassby and Platt 1976; Platt *et al*. 1980; Henley (1993), as cited by Borlongan *et al*. (2017)]. The maximum net photosynthesis was computed as:

$$P_{n\ max} = P_{g\ max} - R_d \quad (3)$$

The saturation irradiance $I_k$ and compensation irradiance $I_c$ were computed, respectively, as:

$$I_k = P_{g\ max}/\alpha \quad (4)$$

$$I_c = P_{g\ max}[(ln(P_{g\ max})/(R_d - P_{g\ max}))/\alpha] \quad (5)$$

**Linking Thallus Morphology (FFGs) with P-I Curves**

We have initially grouped our 50 macroalgal species into functional-forms based on the six groups of Littler and Arnold (1982): [A] sheet, [B] delicately branched filamentous, [C] coarsely branched, [D] thick blades leathery, [E] jointed calcareous, and [F] crustose. The last group (FFG F: crustose) was not represented in our collection. Eleven (11) genera (*i.e. Ulva*, *Chaetomorpha*, *Dictyota*, *Laurencia*, *Sargassum*, *etc.*) were common with their 62 macrophyte species, but only two of our 50 species (*Ulva intestinalis* and *Colpomenia sinuosa*) were among their listed macrophytes. The rest of our species could not be easily fitted into their defined functional-form groups. According to Littler and Arnold (1982), the scheme should not be viewed as representing discrete differences between groups but as mid-points along a continuous gradient of possible thallus types. Thus, after further examination of our species morphological characteristics, they were assigned to the closest functional-form group based on their affinity to the group morphological and physiological characteristics, as was similarly done by Philipps *et al*. (1997) and de los Santos *et al*. (2009). We have further expanded the characterization of our functional-form groups – following that of Balata *et al*. (2011) – by taking close attention to thallus thickness (*vis-à-vis* number of cell layers, cortication, *etc.*), particularly on the bladed or foliaceous forms; "coarseness of branches" due to the presence of numerous simple or complex determinate branchlets or ramuli; the complexity of branching patterns [functional geometry model of Hay (1986)]; and degree of calcification, as inferred by the intensity of bubbles resulting from acid testing on calcified thalli.

After each species has been assigned its functional grouping, the P-I curve parameters – including $P^n_{max}$, $I_k$, $I_c$, α, and $R_d$, of each species – was compiled with the mean taken for each functional group.

**Statistical Analysis**

All data representing P-I curve parameters were tested for normality using the Shapiro-Wilk test and were log-transformed to conform with the parametric assumptions. One-way analysis of variance (ANOVA) was then used to evaluate significant differences between means of the P-I curve parameters among the functional-form groups. If the difference was significant, Tukey's honestly significant difference (HSD) test was further used for *post hoc* analysis to find the significant groupings. All statistical analyses were performed using R software version 3.2.0 (R Core Team 2015), with the significant level set at $p = 0.05$.

## RESULTS

**Functional-Morphology Groupings**

Table 1 presents the 50 macroalgal species categorized into five functional-form groups based on expanded morphological attributes. Their corresponding productivity values expressed as maximum net photosynthetic rates at light saturation ($P^n_{max}$) are graphically shown in Figure 1. Table 1 also lists the P-I curve parameters of each species with the mean values of these parameters within each functional-form group presented in Table 2. Figure 2 presents the P-I curves of representative species from each of the functional-form groups. ANOVA results indicate significant differences in all the P-I curve parameters among groups (Table 2). Mean $P^n_{max}$ among the five functional-form groups are all significantly different, but such is not the case with the other parameters $I_k$, $I_c$, α, and $R_d$ with different significant groupings detected. The morphological characteristics of the functional-form groups, and their P-I curve parameters are further described in the succeeding paragraphs.

**Table 1.** Functional-form grouping (FFG) of the 50 macroalgal species and their P-I curve parameters. Species list within each functional-form grouping is ranked from highest to lowest based on the maximum net photosynthetic rate, $P^n_{max}$.

| | FFG | Macroalgal species | P-I curve parameters | | | | |
|---|---|---|---|---|---|---|---|
| | | | $P^n_{max}$ ($mgO_2$ $gdw^{-1}$ $h^{-1}$) | $I_k$ (µmol photons $m^{-2}$ $s^{-1}$) | $I_c$ (µmol photons $m^{-2}$ $s^{-1}$) | α (mg $O_2$ $gdw^{-1}$ $h^{-1}$/ µmol photons $m^{-2}$ $s^{-1}$) | $R_d$ ($mgO_2$ $gdw^{-1}$ $h^{-1}$) |
| **FFG A: very thin tubes/sheets/strips** | | | | | | | |
| 1 | *A* | *Dictyota cervicornis* Kützing | 69.44 | 56 | 6 | 0.75 | 7.75 |
| 2 | *A* | *Dictyota divaricata* (J.Ag.) J. Ag. | 61.46 | 48 | 1 | 0.80 | -0.80 |
| 3 | *A* | *Ulva lactuca* L. | 59.02 | 135 | 7 | 0.46 | 3.23 |
| 4 | *A* | *Ulva reticulata* Forsskål | 54.57 | 86 | 4 | 0.71 | 2.81 |
| 5 | *A* | *Ulva intestinalis* L. | 48.99 | 9 | 1 | 0.26 | 6.14 |
| **FFG B: thin sheets/delicately branched** | | | | | | | |
| 6 | *B* | *Hydroclathrus clathratus* (C.Ag.) M.Howe | 44.66 | 68 | 4 | 0.72 | 2.73 |
| 7 | *B* | *Halymenia durvillei* Bory | 43.93 | 134 | 6 | 0.35 | 2.14 |
| 8 | *B* | *Anadyomene plicata* C.Ag. | 38.52 | 210 | 10 | 0.20 | 2.02 |
| 9 | *B* | *Chaetomorpha crassa* (C.Ag.) Kützing | 36.84 | 81 | 6 | 0.49 | 2.63 |
| 10 | *B* | *Padina australis* Hauck | 34.81 | 123 | 8 | 0.31 | 2.22 |
| 11 | *B* | *Portieria hornemannii* (Lyngbye) P.C.Silva | 34.16 | 98 | 6 | 0.42 | 2.22 |
| 12 | *B* | *Hypnea cervicornis* J.Ag. | 33.53 | 70 | 10 | 0.64 | 6.18 |
| 13 | *B* | *Caulerpa serrulata* (Forsskål) J.Ag. | 24.19 | 160 | 14 | 0.17 | 2.24 |
| 14 | *B* | *Chlorodesmis fastigiata* (C.Ag.) S.C.Ducker | 20.31 | 72 | 6 | 0.31 | 1.76 |
| 15 | *B* | *Spyridia filamentosa* (Wulfen) Harvey | 18.74 | 19 | 0 | 0.86 | 0.19 |
| **FFG C: medium thick blade/coarsely branched with dense ramuli** | | | | | | | |
| 16 | *C* | *Rhodymenia* sp. | 18.82 | 95 | 8 | 0.22 | 1.66 |
| 17 | *C* | *Turbinaria conoides* (J.Ag.) Kützing | 18.46 | 155 | 1 | 0.12 | 0.16 |
| 18 | *C* | *Colpomenia sinuosa* (Mertens ex Roth) Derbès & Solier | 17.99 | 11 | 2 | 0.07 | 4.50 |
| 19 | *C* | *Gracilaria textorii* (Suringar) Hariot | 17.14 | 19 | 3 | 0.15 | 3.11 |
| 20 | *C* | *Sargassum* sp. 2 | 16.63 | 150 | 21 | 0.13 | 2.64 |
| 21 | *C* | *Caulerpa sertularioides* (S.G.Gmelin) M.Howe | 16.07 | 84 | 3 | 0.49 | 1.17 |
| 22 | *C* | *Sargassum* sp. 1 | 14.85 | 176 | 10 | 0.09 | 0.84 |
| 23 | *C* | *Gracilaria edulis* (S.G.Gmelin) P.C.Silva | 13.46 | 90 | 11 | 0.17 | 1.75 |
| 24 | *C* | *Laurencia similis* K.W.Nam & Y.Saito | 13.38 | 22 | 4 | 0.75 | 2.81 |
| 25 | *C* | *Hormophysa cuneiformis* (S.G.Gmelin) P.C.Silva | 12.67 | 135 | 7 | 0.11 | 0.61 |
| 26 | *C* | *Palisada perforata* (Bory) K.W.Nam- | 12.14 | 46 | 4 | 0.31 | 1.29 |

**Table 1** Cont.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 27 | *C* | *Acanthophora spicifera* (M.Vahl) Børgesen | 11.54 | 26 | 6 | 0.57 | 3.22 |
| 28 | *C* | *Ohelopapa flexilis* (Setchell) F.Rousseau, Martin-Lescanne, Payri & L.Le Gall | 10.29 | 63 | 5 | 0.19 | 0.99 |
| 29 | *C* | *Caulerpa racemosa* (Forsskål) J.Ag. | 8.81 | 99 | 18 | 0.11 | 2.05 |
| 30 | *C* | *Boergesenia forbesii* (Harvey) Feldmann | 8.39 | 169 | 30 | 0.06 | 1.90 |
| 31 | *C* | *Gelidiella acerosa* (Forsskål) Feldmann & Hamel | 8.34 | 122 | 15 | 0.09 | 1.23 |
| 32 | *C* | *Dictyosphaeria versluysii* Weber Bosse | 8.30 | 103 | 32 | 0.12 | 3.47 |
| 33 | *C* | *Turbinaria ornata* (Turner) J.Ag. | 8.16 | 176 | 16 | 0.05 | 0.83 |
| 34 | *C* | *Caulerpa lentillifera* J.Ag. | 8.13 | 226 | 13 | 0.04 | 0.49 |
| **FFG D: heavily thick branches/segments or with moderate calcification** | | | | | | | |
| 35 | *D* | *Tricleocarpa fragilis* (L.) Huisman & R.A.Townsend | 12.77 | 95 | 13 | 0.16 | 1.96 |
| 36 | *D* | *Ganonema farinosum* (J.V.Lamouroux) K.-C.Fan & Y.-C.Wang | 11.81 | 99 | 19 | 0.15 | 2.82 |
| 37 | *D* | *Halimeda discoidea* Decaisne | 11.40 | 125 | 11 | 0.11 | 1.17 |
| 38 | *D* | *Mastophora rosea* (C.Ag.) Setchell | 9.74 | 19 | 2 | 0.57 | 1.15 |
| 39 | *D* | *Halimeda macroloba* Decaisne | 7.17 | 197 | 32 | 0.05 | 1.57 |
| 40 | *D* | *Gracilaria salicornia* (C.Ag.) E.Y.Dawson | 6.49 | 54 | 9 | 0.23 | 2.26 |
| 41 | *D* | *Kappaphycus cottonii* (Weber Bosse) Doty *ex* H.D.Nguyen & Q.N.Huyn | 6.26 | 63 | 3 | 0.12 | 0.39 |
| 42 | *D* | *Ceratodictyon spongiosum* Zanardini | 5.10 | 271 | 70 | 0.02 | 1.73 |
| 43 | *D* | *Gracilaria eucheumatoides* Harvey | 3.33 | 45 | 9 | 0.14 | 0.83 |
| **FFG E: heavily calcified** | | | | | | | |
| 44 | *E* | *Actinotrichia fragilis* (Forsskål) Børgesen | 8.81 | 71 | 1 | 0.13 | 0.17 |
| 45 | *E* | *Udotea orientalis* A.Gepp & E.S.Gepp | 7.62 | 65 | 10 | 0.14 | 1.51 |
| 46 | *E* | *Galaxaura divaricata* (L.) Huisman & R.A.Townsend | 4.05 | 14 | 2 | 0.34 | 0.71 |
| 47 | *E* | *Galaxaura rugosa* (J.Ellis & Solander) J.V.Lamouroux | 4.03 | 50 | 11 | 0.10 | 1.06 |
| 48 | *E* | *Amphiroa fragilissima* (L.) J.V.Lamouroux | 3.03 | 9 | 2 | 0.45 | 0.87 |
| 49 | *E* | *Halicoryne wrightii* Harvey | 2.85 | 54 | 7 | 0.22 | 0.34 |
| 50 | *E* | *Amphiroa foliacea* J.V.Lamouroux | 1.68 | 10 | 3 | 0.24 | 0.62 |

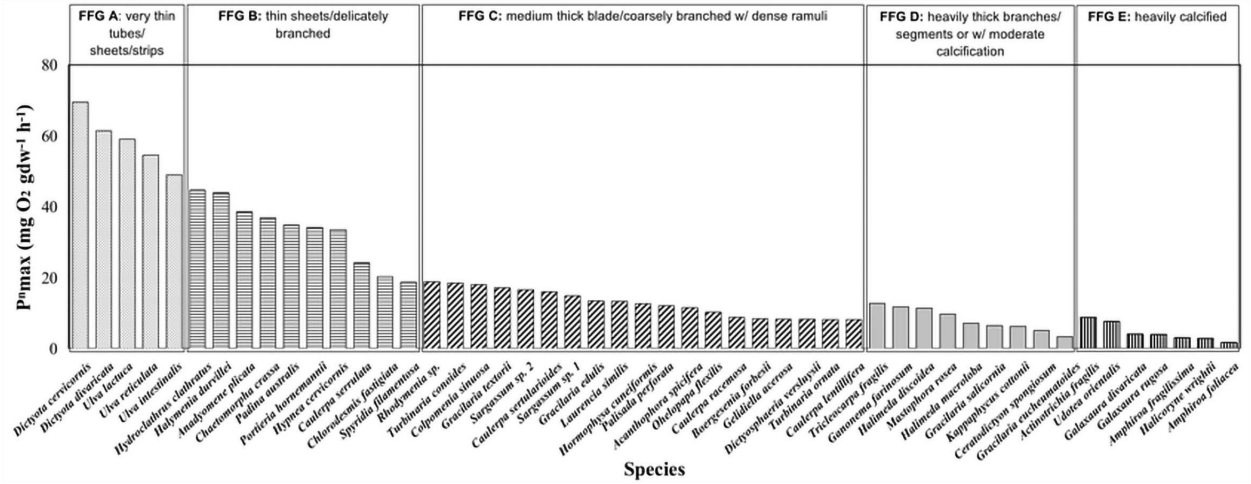


**Figure 1.** The ranking of maximum net photosynthetic rate from highest to lowest of member macroalgal species of the five FFGs.

**Table 2.** Mean (± SD) values of the P-I curve parameters of the five FFGs (A–E). ANOVA results indicated a significant difference among functional form groups in all parameters ($p < 0.05$). Tukey HSD test identified significant groupings, as indicated by the different letters next to each value.

| FFG | P-I curve parameters | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $P^n_{max}$ | | $I_k$ | | $I_c$ | | α | | $R_d$ | |
| | ($mgO_2$ $gdw^{-1}$ $h^{-1}$) | | (μmol photons $m^{-2}$ $s^{-1}$) | | (μmol photons $m^{-2}$ $s^{-1}$) | | (mg $O_2$ $gdw^{-1}$ $h^{-1}$/μmol photons $m^{-2}$ $s^{-1}$) | | ($mgO_2$ $gdw^{-1}$ $h^{-1}$) | |
| **A** | 58.70 ± 9.67 | a | 67 ± 45 | a | 3 ± 3 | c | 0.60 ± 0.22 | a | 3.83 ± 3.35 | c |
| **B** | 32.97 ± 9.47 | b | 103 ± 57 | a | 7 ± 4 | bc | 0.45 ± 0.24 | b | 2.43 ± 1.62 | b |
| **C** | 12.82 ± 4.02 | c | 104 ± 67 | a | 11 ± 10 | ba | 0.20 ± 0.22 | c | 1.83 ± 1.54 | b |
| **D** | 8.23 ± 2.99 | d | 100 ± 80 | a | 16 ± 20 | a | 0.17 ± 0.15 | c | 1.41 ± 1.21 | ba |
| **E** | 3.13 ± 0.92 | e | 27 ± 35 | b | 5 ± 6 | bc | 0.27 ± 0.15 | c | 0.72 ± 0.40 | a |

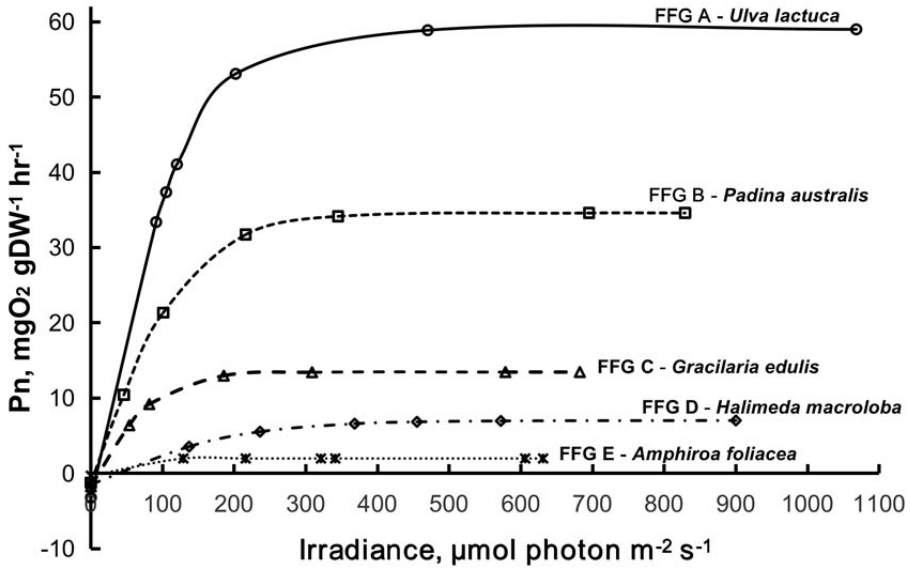


**Figure 2.** The P-I curve of representative species per FFG.

***FFG A: very thin tubes/sheets/strips:*** Five species were categorized in this group for having the thinnest delicate thalli of flat sheets (*Ulva lactuca*), strips (*Dictyota* spp.), or very thin filamentous tubes (*U. intestinalis*). Their P-I curves showed remarkably (Table 2) the steepest mean (± SD) slopes ($\alpha = 0.60 \pm 0.22$ mg $O_2$ gdw$^{-1}$ h$^{-1}$/µmol photons m$^{-2}$ s$^{-1}$), with the highest mean photosynthetic rate ($P^n_{max} = 58.70 \pm 9.67$ mg $O_2$ gdw$^{-1}$ h$^{-1}$) that is twice greater than that of FFG B and several folds greater than those of the rest of the groups (Table 2). The mean saturation irradiance of FFG A ($I_k = 67 \pm 45$ µmol photons m$^{-2}$ s$^{-1}$) – although lower – did not significantly differ from the high values of FFGs B, C, and D, which are all higher than that of FFG E. FFG A mean compensation irradiance was low ($I_c = 3 \pm 3$ µmol photons m$^{-2}$ s$^{-1}$), similar to those of FFGs B and E, and significantly lower than those of FFGs C and D ($p < 0.05$). In contrast, FFG A mean respiration rate ($R_d = 3.83 \pm 3.35$ mg $O_2$ gdw$^{-1}$ h$^{-1}$) was significantly the highest among all functional form groups (Table 2).

***FFG B: thin-bladed frondose thalli/delicately branched.*** The frondose thalli of FFG B were thicker and more complex in structure than FFG A (*e.g. Anadyomene*, *Padina*, *Halymenia*, *Portieria*). *Caulerpa serrulata*, because of its laminar erect fronds, is categorized to belong to this group. The delicately branched forms have thin branches and simple cortication (*e.g. Hypnea cervicornis*, *Spyridia filamentosa*). This group has the next highest photosynthetic rates ($P^n_{max} = 32.97 \pm 9.47$ mg $O_2$ gdw$^{-1}$ h$^{-1}$) and steepness of the slope ($\alpha = 0.45 \pm 0.24$ mg $O_2$ gdw$^{-1}$ h$^{-1}$/µmol photons m$^{-2}$ s$^{-1}$) (Table 2). Their mean saturation irradiance was generally high ($I_k = 103 \pm 57$ µmol photons m$^{-2}$ s$^{-1}$), not significantly different from those of the other functional-form groups except FFG E, which has a significantly lower value. FFG B mean compensation irradiance ($I_c = 7 \pm 4$ µmol photons m$^{-2}$ s$^{-1}$) was also low, similar to those of FFGs A and E, but significantly lower than those of FFGs C and D. Their respiration rate ($R_d = 2.43 \pm 1.62$ mg $O_2$ gdw$^{-1}$ h$^{-1}$) was not significantly different from those of FFG C, and FFG D was 0.5-fold lower than that of FFG A and about three-fold greater than that of FFG E (Table 2).

***FFG C: medium thick blades/coarsely branched with dense ramuli.*** This group is the most morphologically diverse consisting 40% of the macroalgae collected in the present study. Since only young blades of the large brown macroalgae (*i.e. Sargassum* spp., *Turbinaria* spp., *Hormophysa cuneiformis*) were used in the experiment, these species were classified under this FFG as their blade morphology resembles that of the other species in this group. Species in this group have blades that are thicker than those in FFG A and FFG B but thinner than the frondose species of FFG D. Their branching forms have axes clothed with dense short determinate branchlets or ramuli (*e.g. Laurencia similis*, *Ohelopapa flexilis, Palisada perforata, Caulerpa* spp., *Acanthophora spicifera*, and *Gelidiella acerosa*). Sacccate (*e.g. Colpomenia sinuosa, Dictyosphaeria versluysii*) and vesiculate (*e.g. Boergesenia forbesii*) forms were also categorized here. Their mean photosynthetic rate ($P^n_{max} = 12.82 \pm 4.02$ mg $O_2$ gdw$^{-1}$ h$^{-1}$) was several folds lower than those of FFGs A and B but higher than those of FFGS D and E. Their P-I curve showed a gentler slope ($\alpha = 0.20 \pm 0.22$ mg $O_2$ gdw$^{-1}$ h$^{-1}$/µmol photons m$^{-2}$ s$^{-1}$) that is significantly less than those of FFGs A and B but similar to those of FFGs D and E. Their mean saturation irradiance was high ($I_k = 104 \pm 67$ µmol photons m$^{-2}$ s$^{-1}$) but not significantly different from those of the other functional-form groups except FFG E. Their mean compensation irradiance ($I_c = 11 \pm 10$ µmol photons m$^{-2}$ s$^{-1}$) varied widely among members, and the mean value differed significantly from those of FFGs A and E. Their mean respiration rate ($R_d = 1.83 \pm 1.54$ mg $O_2$ gdw$^{-1}$ h$^{-1}$) was not significantly different from those of FFGs B and D, was 0.5-fold lower than that of FFG A, and about two-fold greater than that of FFG E (Table 2).

***FFG D: thalli with heavily thick branches/segments or with moderate calcification.*** This group included species with moderate calcification, *i.e. Halimeda* spp. and *Mastophora rosea,* and only young parts were used as test samples. Also included in this group were those with very thick branches or segments, *e.g. Ceratodictyon spongiosum, Gracilaria eucheumatoides*, *G. salicornia*, and *Kappaphycus cottonii*. Their mean photosynthetic rate ($P^n_{max} = 8.23 + 2.99$ mg $O_2$ gdw$^{-1}$ h$^{-1}$) was significantly lower than those of FFGs A, B, and C but higher than that of FFG E. Their P-I curve showed a gradual slope ($\alpha = 0.17 \pm 0.15$ mg $O_2$ gdw$^{-1}$ h$^{-1}$/µmol photons m$^{-2}$ s$^{-1}$), similar to those of the coarsely branched FFG C and heavily calcified FFG E, and was significantly lower than those of the thin-bladed and delicately branched FFGs A and B. Their mean saturation irradiance was high ($I_k = 100 \pm 80$ µmol photons m$^{-2}$ s$^{-1}$), but not significantly different from those of the other functional form groups except FFG E. Their mean compensation irradiance ($I_c = 16 \pm 20$ µmol photons m$^{-2}$ s$^{-1}$) was the highest among all functional form groups and was significantly similar only with that of FFG C. Mean respiration rate in this group ($R_d = 1.41 \pm 1.21$ mg $O_2$ gdw$^{-1}$ h$^{-1}$) was similar to those of the other functional-form groups except the higher rate of FFG A.

***FFG E: with heavily calcified thalli.*** Heavy calcification characterizes the members of this group, most of which belong to the rhodophyte genera, *i.e. Actinotrichia, Amphiroa* spp., *Galaxaura* spp., and a few chlorophyte species, *i.e. Halicoryne wrightii* and *Udotea orientalis*.

The group recorded the lowest mean photosynthetic rates ($P^n_{max}$ = 3.13 + 0.92 mg $O_2$ $gdw^{-1}$ $h^{-1}$). Their P-I curve had a gradual slope (α = 0.27 + 0.15 mg $O_2$ $gdw^{-1}$ $h^{-1}$/ µmol photons $m^{-2}$ $s^{-1}$) – similar to the coarsely branched, thick-bladed, and lightly calcified members of FFGs C and D. Unlike the rest of the functional-form groups, they saturated at the lowest irradiances ($I_k$ = 27 ± 35 µmol photons $m^{-2}$ $s^{-1}$). Their mean compensation irradiance was also low ($I_c$ = 5 ± 6 µmol photons $m^{-2}$ $s^{-1}$), similar to those of the thin-bladed and delicately branched FFGs A and B. Dark respiration rate ($R_d$ = 0.72 ± 0.40 mg $O_2$ $gdw^{-1}$ $h^{-1}$) was lowest in this group, although this was not significantly different from that of FFG D (Table 2).

**Thallus Morphology and P-I Curve Parameters**

A significant decreasing trend was evident particularly in the $P^n_{max}$ values – highest in FFG A, thallus form with very thin construction, then gradually decreasing to reach the lowest rate in FFG E, the thallus form with thick or heavy calcification. The thallus forms with thinner blades (FFGs A and B) also had the steepest slopes (high mean α values), whereas the rest of the thallus forms (FFGs C, D, and E) had gentle slopes (low mean α values). Saturation irradiances ($I_k$ values) of FFGs A–D were high and varied quite widely among the members, whereas their values were significantly higher than the low value of FFG E. The thin thallus forms (FFGs A and B) and the heavily calcified forms (FFG E) had low mean compensation irradiances compared with FFGs C and D. Mean dark respiration rate ($R_d$) was the highest in the thinnest thallus forms (FFG A) and the lowest in the heavily calcified forms (FFG E). Photoinhibition of photosynthesis was not exhibited by any of the species, even at the highest irradiance recorded during incubation (about 1,500 µmol photons $m^{-2}$ $s^{-1}$).

## DISCUSSION

**Functional-Morphology Grouping**

Our results, based on the ranking and grouping of 50 macroalgal species into functional-form groups, tend to support the functional-form hypothesis of Littler (1980) and Littler and Arnold (1982), which predicts that the thin and delicately branched forms of macroalgae have higher productivity than forms that are coarsely branched and highly calcified, as evidenced by their measured $P_{max}$ values. It was not easy to clearly fit our species into their defined functional-form in reference to the brief description of their morphological characteristics. Philipps *et al.* (1997) likewise encountered a similar problem with their species, in which 14 of their 82 algal species were difficult to be classified into functional groups. Differences in geographical regions and habitats of our study in comparison with most published studies from temperate areas could have affected not only the species composition but also differences in thallus morphology of similar taxa (*e.g. Sargassum*, *Padina*). For instance, similar in genus but different in species, our *Padina* species (*P. australis*) was classified in FFG B for having thin sheets, whereas *P. durvillei* Bory of Littler and Arnold (1982) was in FFG D for having thick blades. Littler (1980) and Littler and Arnold (1982) classified all their articulated corallines into one functional form group E, *i.e.* jointed calcareous. But in our case, only those jointed corallines with heavy calcification were included in FFG E (Table 1), along with other heavily calcified rhodophytes (Family Galaxauraceae) and chlorophytes not present in their sites. *Mastophora rosea*, a foliaceous articulated coralline with compressed thallus and moderate calcification, was categorized into FFG D. Our morphological assignment of the 50 species to fit their predictive function seemed plausible, as shown in Table 2, although the responses of individual species were not always predicted to correspond to the responses of their assigned functional group (Table 1; Figure 1). Our groupings were based on morphological characters with productivity as the inferred function. Validation using $P^n_{max}$ parameter of the P-I curve showed that thickness of thallus blades, coarseness of branches, complex branching, and calcification appeared to lessen photosynthetic capacity, as shown by the significantly decreasing trend of $P^n$max from FFGs A–E.

**FFGs and P-I Curve Parameters**

***FFG A.*** Species belonging to this group had the highest productivity coinciding with their extremely thin thallus structure in agreement with the results of Littler and Murray (1974), Littler (1980), Littler and Littler (1980), Littler and Arnold (1982), Littler *et al.* (1983), Rosenberg *et al*. (1995), and de los Santos *et al*. (2009). Thalli that are thin in construction have high photosynthetic rates per unit of biomass (Falkowski and Raven 1997), not only because nearly all of the cells are photosynthetic but also of their direct access to carbon supplies and nutrients in the water (Hurd *et al.* 2014). Moreover, their cells are thinner-walled than most other coarser forms which – according to Littler (1980), Littler and Arnold (1982), and Hay (1986) – minimize self-shading of the internal photosynthetic apparatus, thus promoting higher productivity. This thallus morphology, which allowed maximum surface area for light absorption, also resulted in the highest α values measured in this group. Arnold and Murray (1980), Johansson and Snoeijs (2002), and Gomez *et al*. (2004) likewise have measured high $P_{max}$ and α values in their morphologically thin-sheet macroalgal species. A high α value is a measure of the species' efficiency to photosynthesize under low light conditions (Cheshire *et*

*al.* 1996), such as during cloudy or stormy days or even during early morning or late afternoon when natural light is low. Moreover, low values of their compensation irradiances indicated their capacity to survive in habitats with low photon flux densities, such as when covered or smothered with silt or sand, especially during monsoon seasons, or when occurring in shade (*i.e.* under rocks or under a canopy of larger macrophytes).

***FFG B.*** This group with the next highest productivity had thalli of thin frondose blades that were thicker than FFG A members; others were delicately branched or were uniseriate with thick walls. The bladed forms had more cell layers or tissues (*i.e. Padina australis*, *Halymenia durvillei*, and *Portieria hornemannii*) or were formed of interwoven filaments (*i.e. Anadyomene plicata*) that thickened the thallus. This probably decreased their surface area to volume or biomass ratio, thus resulting in a decrease in photosynthetic capacity compared to the extremely thin thallus structure of FFG A. On the basis of surface area: volume ratios, filamentous algae should have had higher productivity, but clumping among the uniseriate filaments of *Chaetomorpha crassa* may have promoted self-shading of the photosynthetic apparatus – resulting in the lowering of its photosynthetic capacity, as was also reported for *C. linum* (O.F.Müller) Kützing by Krause-Jensen *et al.* (1996). On the other hand, the reticulate nature of *H. clathratus* compared to related species – *Colpomenia sinuosa* (categorized into FFG C), which was also fleshy but saccate and saxicolous – could have the advantage of allowing light to pass through its holes and improve access to its photosynthetic cells. According to Ramus (1990), multi-cellular tissues of algae consist of different ranges of cell types and air spaces promoting photon gradients with a varying magnitude of back and forward scattering conditions. Although finely branched, the flaccid multi-layered thallus construction in *Hypnea cervicornis* and *Spyridia filamentosa* could have increased self-shading that lowered their photosynthetic capacity compared with the FFG A species.

***FFG C.*** This is the most morphologically diverse group whose members varied from monolayered foliose sheets to multi-layered branches, coarsely branched forms, or those with a clumped habit, *etc.* This diversity in form did not correlate well with the surface area to volume or biomass hypotheses, consistent with the findings of Littler (1980) and Littler and Arnold (1982). The multi-layering arrangement of the dense determinate branchlets in the species, *i.e. Palisada perforata*, *Laurencia similis*, *Acanthophora spicifera*, *Caulerpa lentillifera*, *C. sertularioides*, *etc.*, the clumpy and saxicolous habit of *Boergesenia forbesii* and *Colpomenia sinuosa* accounted for the difficult estimation of these ratios. These forms were exceptions to the usual pattern (Dawes *et al*. 1978; Littler 1980; Littler and Arnold 1982) that resulted in increased self-shading and intraspecific competition for nutrients as an adaptive strategy against predation, desiccation, or thermal stress (Hay 1981; Taylor and Hay 1984) in exchange for lessened efficiency in acquiring light energy, thereby reducing photosynthetic capacity compared to FFGs A and B.

***FFG D.*** The high proportion of structural, non-photosynthetic materials in the members of this group is postulated to have contributed to their low photosynthetic capacity, thus, low in productivity as suggested by Dawes (1998), Littler (1980), and Littler *et al.* (1983) compared to FFGs A, B, and C. This high proportion of structural, non-photosynthetic materials is due to moderate calcification in *Ganonema*, *Mastophora*, *Tricleocarpa*, and *Halimeda* spp.; the polysaccharide outer layer in K*appaphycus cottonii*, *Gracilaria eucheumatoides*, and *G.salicornia*; and the amount of medullary tissue among the latter corticated members. According to Gomez and Huovinen (2012), seaweeds can be morphologically complex and, hence, carbon metabolism and its products are functionally integrated with their growth patterns (*e.g.* channeling resources to calcium carbonate or polysaccharide production). The gentle slope of their P-I curve (low α) is indicative of their low photosynthetic efficiency, thereby requiring a high level of irradiance to reach photosynthetic saturation. Being intertidal species, these non-photosynthetic materials could be their structural investment to withstand desiccation, resistance to wave action, and protection from grazing (Schonbeck and Norton 1979; Littler and Littler 1980; Littler *et al*. 1983; Taylor and Hay 1984; Dudgeon and Johnson 1992; Flores-Molina *et al.* 2014).

***FFG E.*** This group, which registered the lowest photosynthetic rates, had thalli made up of a high ratio of structural material to photosynthetic tissue (Littler 1980), much of which exhibited low metabolic rates (Kanwisher 1966; Kremer 1980; Littler 1980; Littler and Arnold 1982), thus resulting in the lowest net productivity. The differential allocation of resources and energy of photosynthesis to structural tissues (*i.e.* calcification) greatly affects the lowering of productivity (Dawes 1998; Littler 1980; Littler *et al*. 1983). Experiments conducted on their diurnal photosynthetic pattern [Saco and Ganzon-Fortes (2014), unpublished data] revealed that, although low in $P^n_{max}$, photosynthesis in this functional-form was consistently maximal from sunrise until sunset, indicating their capacity to operate at full photosynthetic capacity even at low light regimes, which – in nature – may occur near dusk or dawn, or under shaded conditions. Their low compensation irradiance similar to FFG A is indicative of their adaptive capacity to habitats receiving low

irradiance. According to Dayton (1975), these responses are suggestive of ecologically obligate understory species or canopy species adapted to lower irradiance. The high degree of calcification that reduced productivity (Raven and Geider 2003) could be a survival strategy for this morphological form, as related members were found to be resistant to grazing due to non-palatability and were resistant to mechanical stress (Littler and Littler 1980; Littler *et al*. 1983).

**Thallus Morphology and P-I Curve Parameters**

Using P-I curves, our study demonstrated that the maximum net photosynthetic rate and the initial slope of the curve (α) declined with increasing thallus thickness or complexity. As reported by Arnold and Murray (1980) on their materials from Laguna Beach, California, the thin, sheet-like thalli like *Ulva* spp. have the highest $P_{max}$ and steepest α compared to the optically dense *Codium fragile* (Suringar) Hariot, which has the lowest $P_{max}$ and the most gradual slope. Littler (1980) detected that forms with relatively higher proportions of photosynthetic tissue (*e.g.* thin and finely-branched forms) tended to have higher absolute rates of respiration. This rate decreases with increasing thallus thickness and complexity, such that those forms with greater proportions of structural tissues (*e.g.* calcified forms) result in proportionately greater ratios of respiration to photosynthesis, indicating that much of the structural material is non-metabolic. The exceptionally low respiration rates shown by most of the coralline algae on a weight basis would seem to support this interpretation (Littler 1980), as was also observed in our FFG E materials (heavily calcified forms). Enriquez *et al*. (1996) observed that respiration declined with increasing thickness of photosynthetic structures, and this decline was steeper for photosynthesis than for respiration. Dangan-Galon *et al*. (2013) – analyzing only the $P_{max}$ data of P-I curves obtained from three species from Bolinao, Pangasinan, and one from Calatagan, Batangas, Philippines – reported that *U. lactuca*, having a thin sheet form, has the highest oxygen production rate over the branching-forms (*i.e. G. edulis*, *K. striatus*, and *Ganonema farinosum*). Calcification in *G. farinosum* was suspected to have influenced its lowest $P_{max}$ value.

None of the 50 macroalgal species examined in the present study was photoinhibited by irradiance up to 1,500 µmol photons $m^{-2}$ $s^{-1}$. In the site where these species were collected, irradiance could reach 2,000 µmol photons $m^{-2}$ $s^{-1}$ on cloudless summer days and several folds less during cloudy and rainy days. Being inhabitants of this shallow intertidal zone, these species have been exposed to high and low levels of irradiance. The saturation irradiance varied widely among members of FFGs A–D and did not show significant differences in their mean values except with the heavily calcified FFG E, which registered the lowest mean value. Similar findings were reported by Arnold and Murray (1980) on their six species morphologically categorized also in FFGs A–D – *Ulva* spp., *C. linum*, and *Codium*. Their materials were also collected in shallow littoral zones, where light regimes could vary greatly from exposed to shaded (as under rocks or under canopies of foliose macrophytes). Moreover, exposure of these marine habitats to considerable diurnal changes in the impinging photon fluence rates due to the position of the sun, cloudliness, and the tides (Hanelt and Nultsch 2002) could further enhance variations in the light regimes in the intertidal areas. Wave action could also lower photon flux densities in seaweed habitats by stirring up sediments, thus smothering the thalli or even dislodging small to medium-sized rocks (Wing and Patterson 1993), especially during monsoon seasons. Thus, the light exposure history of a species could affect its adaptation or acclimation capacity (Ramus and Rosenberg 1980).

No trend was detected that correlated compensation irradiance with thallus morphology, as was also observed by Arnold and Murray (1980) and Johansson and Snoeijs (2002). Dawes (1992) had similar findings with his eucheumatoid materials. Gomez *et al*. (1997) reported that in five Antarctic macroalgal species, compensation and saturation irradiances can decrease as acclimation to ambient light with lower values at greater depths and these were not influenced by their thallus morphology.

Other factors (*e.g.* pigment levels, nutrient uptake rates) could have affected seaweed responses to ambient light conditions. Seaweeds manipulate their light-harvesting capacity (Ramus *et al*. 1976) not to maximize photosynthesis but rather to optimize it, regardless of ambient light conditions, to meet the energy requirement for their growth. According to Hanelt and Figueroa (2012), under low light, the plant invests more energy in the synthesis of light-collecting pigments. This incurs a high energy-cost in their production per unit light absorption rate in a given underwater spectrum (Raven and Geider 2003). Production of pigments is an energy consuming reaction which uses an increasing fraction of energy input when irradiance decreases (Raven *et al*. 2000). For a certain time period net photosynthetic rates need to be high enough so that seaweeds can promote growth, reproduction, as well as have enough energy for storage to cope with reduced light availability (Hanelt and Figueroa 2012).

The present study has demonstrated the use of P-I curves to further support the hypothesis that morphological form and certain physiological functions of photosynthesis are linked in macroalgae. It would, thus, be possible to predict the general photosynthetic responses of an alga based on its morphology. Exceptions or contradictions to this may exist (Padilla and Allen 2000), yet the

functional-form group approach is practical in predicting the outcome of productivity in related ecological studies. However, some cautions are needed when predicting the species contribution to reef productivity, as there could be intrinsic variation in photosynthetic responses within different morphological parts of the same thallus (*e.g.* young *vs.* old parts or apical *vs.* basal parts) and /or habitat. Improved knowledge of macroalgal taxonomy and morphology would prove useful in assigning species to their respective functional-form groups, as was done for the majority of our 50 macroalgal species. Lastly, P-I curve data determined for each species could be useful for culture studies. In particular, the $I_k$ data could provide insights into the level of irradiance to be used for growth experiments. This will be particularly relevant if any of these species will be further explored for their mariculture potential in the future.

## ACKNOWLEDGMENTS

Appreciation is extended to: [1] the Philippine Council for Aquatic, Agricultural, and Natural Resources Research and Development of the Department of Science and Technology as thesis grant to the first author; [2] the UP-CS-MSI research grant to the second author; [3] the Commission on Higher Education for the financial support; and [4] the staff of the Bolinao Marine Laboratory, UP-MSI, and the Batangas State University for their assistance. Helpful critics and recommendations from Dr. Rhodora Azanza and Dr. Wilfredo Uy are acknowledged, most especially to the late Dr. Ronald Villanueva, to whom this paper is wholeheartedly dedicated. Also, deep appreciation is extended to the reviewers for greatly improving the manuscript of this paper.

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