

Biomass and Relative Coverage of Benthic Algae in the Fore-Reef of Curaçao (Netherlands Antilles) in Relation to Production

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ABSTRACT: Biomass of benthic algae, expressed as chlorophyll a content ($\mu\text{g cm}^{-2}$) and as dry weight (mg cm^{-2}) per substrate surface area in the coral reef of Curaçao at 12 m and 25 m depth was measured from August 1978 to March 1979. To determine dry weights, substrates containing endolithic and epilithic algae were oxidized by means of wet combustion with hydrogen peroxide. Loss of weight caused by this process was regarded as algal dry weight. The crustose corallines *Archaeolithothamnion dimotum* Fosl. et Howe (25 m), *Hydrolithon boergesenii* (Fosl.) Fosl. (12 m and 25 m) and *Lithophyllum cf. intermedium* Fosl. (12 m), vegetations of endolithic algae dominated by *Ostreobium quekettii* Born. et Flah. (12 m and 25 m), and mixed turfs of epilithic filamentous algae and sometimes *Lithophyllum cf. intermedium* on substrates containing endolithic algae (12 m and 25 m) were examined. Chlorophyll a values ranged from $8.7 \mu\text{g cm}^{-2}$ for *H. boergesenii* at 12 m to $20.5 \mu\text{g cm}^{-2}$ for epilithic filamentous algae on substrates containing endolithic algae at 25 m. Dry weights varied from 12.7 mg cm^{-2} for *L. cf. intermedium* at 12 m to 25.7 mg cm^{-2} for epilithic filamentous algae on substrates containing endolithic algae at 25 m. Both at 12 m and at 25 m, differences in chlorophyll a content and dry weights between substrates containing endolithic algae with and without epilithic filamentous algae were low. Biomass of endolithic algae is quantitatively more important than that of epilithic filamentous algae. It is concluded that, at 12 m, biomass of the algal vegetation as a whole is lowest while production is highest. This is attributed to maximum grazing pressure at this depth ('drop off' community), especially on epilithic filamentous algae.

INTRODUCTION

A striking feature of coral reefs is the inconspicuousness of filamentous benthic algae as contrasted with the abundance of other benthic organisms such as corals and crustose corallines and with the abundance of herbivorous animals. The inconspicuousness of this vegetation is now attributed to intensive grazing by herbivorous fishes and sea urchins (Hiatt and Strasburg, 1960; Randall, 1961; Bakus, 1966; van den Hoek, 1969; Earle, 1972; Vine, 1974; van den Hoek et al., 1975, 1978; Ogden, 1976; Wanders, 1976a; Brawley and Adey, 1977). Cage experiments, in which algae were protected against grazing, resulted after some time in the development of a luxuriant vegetation of filamentous algae (Randall, 1961; Bakus, 1967; Earle, 1972; Vine, 1974; Ogden, 1976; Day, 1977; Wanders, 1977). For instance, a small patch reef in the Virgin Islands cleared of all sea urchins was overgrown with a dense cover of algae within 6 months (Ogden et al.,

1973; Ogden and Lobel, 1978). These results support van den Hoek's hypothesis (1969) that undergrazing might cause degradation of the coral reef. Overgrowth of the reef with algae would not only prevent settlement and growth of crustose corallines and juvenile corals but could also kill adult benthic organisms by the entrapment of sediment in the algal mat (Dart, 1972; Vine, 1974; van den Hoek et al., 1975, 1978; Wanders, 1977; Ogden and Lobel, 1978; Brock, 1979). More evidence about the role of herbivorous fishes comes from a comparison of the algal vegetation in and outside the territories of damselfishes. Vine (1974) and Brawley and Adey (1977) found a higher algal biomass inside the territories than outside. Damselfishes are known to defend their territories against other fishes, including herbivorous species (Vine, 1974; Brawley and Adey, 1977; Ogden and Lobel, 1978).

The reef can also be endangered by overgrazing. When the standing stock of filamentous algae is not sufficient to support the large quantities of herbivorous

animals, reef degradation can occur because calcareous substrates and crustose corallines are rasped off (Adey and Vassar, 1975; van den Hoek et al., 1975; Bak, 1976). Moreover, according to Bak and van Eys (1975), *Diadema antillarum* Philippi – a sea-urchin known to be herbivorous – can rasp off living coral tissue as a secondary food source. These observations clearly demonstrate the importance of benthic algae in reef building and degradation processes.

The role of benthic algae in the coral reef of Curaçao has been investigated since 1969 (van den Hoek, 1969). Van den Hoek et al. (1975, 1978) investigated the zonation of algae in relation to that of corals and gorgonians in 2 transects down to 65 m depth. They found that total coverage of fleshy and filamentous algae and of crustose corallines was lowest in the 'drop off community' (6.5–13 m depth) and increased with increasing depth down to 50 m. Wanders (1976a, b, 1977) investigated the role of benthic algae in the shallow reef (0.5 m– 3 m depth). He measured production and biomass of the different vegetation components per unit reef surface. By estimating the mean substrate surface area occupied by the various primary producers per square meter of sea surface he was able to estimate productivity of each of the photosynthetic participants of the reef on an area basis. In addition, he demonstrated the important role of herbivores in the shallow reef with quantitative data. Van den Hoek et al. (1978) emphasize the need for quantitative data on algal growth and herbivorous consumption in the deeper reef zones in order to explain possible relations between grazing and the algal vegetations there. Voooren (1981) measured rates of photosynthesis and respiration of the various vegetation components at 10 m and 25 m depth and de Groot and de Ruyter van Steveninck (unpubl.) measured the relative coverage of the various reef components down to 40 m. In this paper measurements are presented on the biomass of the various vegetation components. A combination of these data on production, biomass and relative coverage permits an estimation of the role of the various primary producers in the deeper reef zones of the coral reef of Curaçao.

MATERIALS AND METHODS

The study area is situated off Klein Piscadera on the leeward South-West coast of Curaçao (Fig. 1). A description of this area and the species composition of its vegetation can be found in van den Hoek et al. (1978: Transect I). The sampled vegetations (Fig. 1) were situated at 12 m depth in the 'drop off community' and at 25 m depth in the 'roof shingle community' (van den Hoek et al., 1978). By means of SCUBA diving,

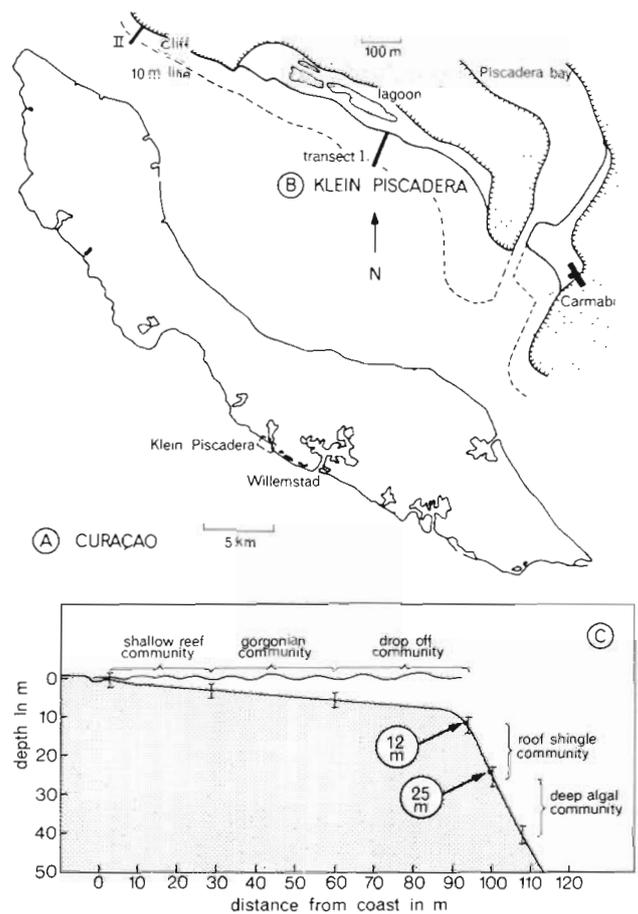


Fig. 1 (A) Map of Curaçao (Netherlands Antilles). (B) Detail of studied area near Klein Piscadera. Vegetation samples were taken from Transect I, relative coverage was estimated in Transects I and II (after de Groot and de Ruyter van Steveninck, unpubl.). (C) Profile of reef near Transect I with zonal communities as distinguished by van den Hoek et al. (1978)

pieces of carbonate substrate with the attached vegetation of epi- and endolithic algae were collected during August 1978 to March 1979. These limestone rocks were removed with hammer and chisel and were used for chlorophyll *a* and dry weight determinations. The most common vegetation components were sampled (Table 1). All vegetation types collected were from elevated positions; sand and coral rubble were not sampled.

Limestone blocks were cut into smaller samples by means of an electric glass-cutting machine. These samples were chosen so that they were representative for the vegetation component as a whole and contained as few animals as possible. Animals present were removed. Samples varied from 8.5–155.8 cm² and were 0.5–2.0 cm thick. Algal species composition was determined and percentage cover of the sample was estimated. For crustose corallines and endolithic algae

Table 1. List of vegetation components sampled at 12 m and at 25 m depth off the South West Coast of Curaçao

1	<i>Archaeolithothamnion dimotum</i> Fosl. et Howe – a crustose coralline alga, monospecific stands; at 25 m
2	<i>Hydrolithon boergesenii</i> (Fosl.) Fosl. – a crustose coralline alga, monospecific stands; at 12 m and 25 m
3	<i>Lithophyllum cf. intermedium</i> Fosl. – a crustose coralline alga, monospecific stands; at 12 m
4	Endolithic algae – various limestone perforating algae. Dominant species: <i>Ostreobium quekettii</i> Born. et Flah. in combination with <i>O. constrictum</i> Lukas and <i>Plectonema terebrans</i> Gom. Coverage of epilithic filamentous algae on the substrate less than 10% of sample's surface. At 12 m and 25 m
5	Epilithic filamentous algae (with <i>Lithophyllum cf. intermedium</i>) on substrates containing endolithic algae – the substrate contains the same limestone perforating algae as in Vegetation Component 4. Coverage of epilithic filamentous algae more than 10% of the sample's surface. At 12 m, <i>Lithophyllum cf. intermedium</i> may cover more than 10% of the sample's surface. Species composition of filamentous algae listed in Table 2. At 12 m and 25 m

percentage coloured surface was taken, for filamentous algae the total area covered by the filaments was estimated. The total area of the sample was determined by wrapping the surface in aluminum foil of known density and weighing the foil (Marsh, 1970). All samples were kept in running seawater and when possible were used the same day as they had been collected.

Chlorophyll a Determinations

Samples were ground in a mortar and extracted in acetone. After filtration over a Whatman GF/C glassfilter, extinction was measured with a Vitatron UPM at wavelengths of 665 and 750 nm (Lorenzen, 1967). Chlorophyll *a*, corrected for phaeophytin, was calculated using the formula in Vollenweider (1969, p. 39) and expressed as μg chlorophyll *a* cm^{-2} . Size, thickness and hardness of the substrate influenced the time and the amount of acetone necessary to extract all chlorophyll *a*. Because of this the amount of acetone used varied from 55–240 ml, and extraction time from 10–15 min.

Dry Weight Determinations

The samples were dried at 90 °C for 1 to 2 weeks, cooled to room temperature in a dessicator and weighed on a balance (Sartorius DP3/200 g). This weight was called W1. All organic material was oxidized by means of wet combustion with H_2O_2 (10–20 % for 1 to 2 weeks at room temperature) and the samples were dried and weighed again. (W2). Since some sand remained after this procedure this also had to be dried and weighed. Different samples were oxidized together in one tray so the dry weight of the sand had to be averaged over the samples (W3). This procedure caused some inaccuracies in the dry weight determinations. Finally, the sample's dry weight was calculated as $W1 - (W2 + W3)$ and expressed as mg cm^{-2} .

It was not possible to remove the different types of algae from their substrates. Hence, the observed values for chlorophyll *a*, as well as for dry weight, refer to a combination of epilithic filamentous algae, or crustose corallines, and endolithic algae present in the substrate. To get an impression of the amount of chlorophyll *a* contributed by the endolithic algae, 2 surveying experiments were carried out. In one experiment epilithic filamentous algae were scraped off a sample from 12 m depth. The remaining limestone (area: 10.46 cm^2) was cut into 2 layers, the top layer 12 mm thick, the bottom layer 8 mm. Of both these layers the chlorophyll *a* content was determined. In the other experiment the chlorophyll *a* content and dry weight of filamentous algae growing on a PVC plate were measured. Of course, the PVC plate did not contain endolithic algae. The plate had been present in the reef at a depth of 22 m for about 5 years (Bak, pers. comm.) and was overgrown by a sparse vegetation of filamentous algae. Two samples were cut out of the plate (116 cm^2 and 118 cm^2 respectively). Species composition and percentage cover were determined and the vegetation was scraped off. One sample was used for chlorophyll *a* determination, the other was dried and weighed.

RESULTS

Species Composition

The species composition of the epilithic filamentous algae is summarized in Table 2. At both depths, *Bryobesia cylindrocarpa* Howe, *Caulerpa vickersiae* Boerg. and *Lyngbia* spp. were dominant. At 25 m, also *Gelidiella trinitatis* Taylor, *Gelidiopsis gracilis* (Kütz.) Vick. and *Polysiphonia* spp. were dominant. The species composition of crustose corallines differed

at 12 m and 25 m (Table 1). At 12 m, *Hydrolithon boergesenii* (Fosl.) Fosl. and *Lithophyllum cf. intermedium* Fosl. were the dominant species; at 25 m,

Table 2. Filamentous algae, found at 12 m and 25 m depth and their estimated abundance. d: dominant (present in more than $\frac{1}{3}$ of the samples from this depth); p: present (present in less than $\frac{1}{3}$ of the samples from this depth); -: absent

Algae	12 m	25 m
Cyanophyceae		
<i>Lyngbya</i> spp.	d	d
Rhodophyceae		
<i>Amphiroa fragilissima</i> (L.) Lamour	-	p
<i>Champia parvula</i> (C. Ag.) Harv.	p	-
<i>Ceramium</i> sp.	p	-
<i>Gelidiella trinitatis</i> Taylor	p	d
<i>Gelidiopsis gracilis</i> (Kütz.) Vick	-	d
<i>Herposiphonia</i> sp.	p	p
<i>Jania adhaerens</i> Lamour	p	p
<i>Polysiphonia</i> sp.	p	d
<i>Pterocladia americana</i> Taylor	-	p
<i>Spermothamnion</i> sp.	p	-
Phaeophyceae		
<i>Dictyota</i> sp.	-	p
<i>Ectocarpus</i> sp.	p	-
<i>Giffordia duchassaingiana</i> (Grün.) Taylor	p	-
<i>Sphacelaria</i> sp.	p	-
Chlorophyceae		
<i>Bryobesia cylindrocarpa</i> Howe	d	d
<i>Bryopsis pennata</i> Lamour	p	p
<i>Caulerpa vickersiae</i> Boerg.	d	d
<i>Chaetomorpha</i> sp.	p	p
<i>Cladophora</i> sp.	p	p
<i>Cladophoropsis membranacea</i> (C. Ag.) Boerg.	-	p
<i>Struvea anastomosans</i> (Harv.) Picc.	p	-

Hydrolithon was accompanied by *Archaeolithothamnion dimotum* Fosl. et Howe. Species composition of endolithic algae was the same at both depths (Table 1). *Ostreobium quekettii* Born. et Flah. was dominant together with *Plectonema terebrans* Gom. and *Ostreobium constrictum* Lukas.

Chlorophyll a

Table 3 shows chlorophyll a values for the different vegetation components at 12 m and 25 m depth. At 12 m, chlorophyll a values were all in the same order of magnitude, the crustose corallines being at the lower, the epilithic filamentous algae on substrates containing endolithic algae at the higher end of the range. Values varied from 8.7 (± 2.4) $\mu\text{g chlorophyll a cm}^{-2}$ for *Hydrolithon boergesenii* to 14.0 (± 3.5) $\mu\text{g cm}^{-2}$ for substrates with epilithic filamentous algae. At 25 m the range of chlorophyll a values was wider than at 12 m. Again, the crustose corallines were at the lower, the substrates with epilithic filamentous algae at the higher end of the range (*Hydrolithon boergesenii*: 8.9 [± 2.4] $\mu\text{g cm}^{-2}$; substrates with epilithic filamentous algae: 20.5 [± 5.6] $\mu\text{g cm}^{-2}$).

Comparison of chlorophyll a values for vegetation components present both at 12 m and at 25 m depth (t-tests) shows that at 25 m substrates with epilithic filamentous algae contain significantly more chlorophyll a per cm^2 ($p < 0.05$). For the other vegetation components the differences are not significant (*Hydrolithon*: $p > 0.90$, endolithic algae: $0.10 < p < 0.20$).

A comparison between the chlorophyll a contents of substrates containing endolithic algae with and without epilithic filamentous algae (vegetation compo-

Table 3. Results of chlorophyll a determinations for different vegetation components at 12 m and 25 m depth. Chlorophyll a content expressed in $\mu\text{g cm}^{-2}$ of substrate surface $\pm 95\%$ confidence interval ($\pm t \cdot \frac{S}{\sqrt{n}}$); n: number of samples

Vegetation component	n	12 m			n	25 m		
		Mean area of samples (cm^2)	Mean %-cover of samples	Chlorophyll a ($\mu\text{g cm}^{-2}$)		Mean area of samples (cm^2)	Mean %-cover of samples	Chlorophyll a ($\mu\text{g cm}^{-2}$)
1 <i>Archaeolithothamnion dimotum</i>	-	-	-	-	9	34	100	11.0 \pm 3.8
2 <i>Hydrolithon boergesenii</i>	9	29	87	8.7 \pm 2.4	7	40	89	8.9 \pm 2.4
3 <i>Lithophyllum cf. intermedium</i>	7	39	100	11.8 \pm 1.9	-	-	-	-
4 Endolithic algae	7	44	100	12.3 \pm 3.5	6	19	100	15.6 \pm 4.4
5 Epilithic filamentous algae (with <i>Lithophyllum cf. intermedium</i>) on substrates containing endolithic algae	16	38	95	14.0 \pm 3.5	6	29	100	20.5 \pm 5.6

nents 5 and 4 respectively, Table 1) reveals no significant differences, neither at 12 m ($0.50 < p < 0.90$), nor at 25 m ($0.10 < p < 0.20$).

Dry Weights

Results of dry weight measurements are presented in Table 4. At 12 m, the differences in dry weight between the various vegetation components are small. Values range from $12.7 (\pm 6.7)$ mg cm⁻² for the crustose coralline *Lithophyllum cf. intermedium* to $15.2 (\pm 6.3)$ mg cm⁻² for substrates with epilithic filamentous algae. At 25 m, the range in dry weight values is wider with the lowest value for *Hydrolithon*: $13.3 (\pm 6.8)$ mg cm⁻² and the highest value for substrates with epilithic filamentous algae: $25.7 (\pm 6.0)$ mg cm⁻².

Comparison of the dry weights of the same vegetation component sampled at different depths shows that for endolithic algae and for substrates bearing epilithic filamentous algae dry weights per cm² are significantly higher at 25 m ($p < 0.05$ and $p < 0.02$ respectively); for *Hydrolithon* there is no significant difference ($0.50 < p < 0.90$).

Dry weights of substrates that contain endolithic algae with and without epilithic filamentous algae (vegetation components 5 and 4 respectively) were not significantly different, both at 12 m ($0.50 < p < 0.90$) and at 25 m depth ($0.50 < p < 0.90$).

Comparative Contributions of Epilithic Filamentous Algae and Endolithic Algae to Total Biomass

Comparison of the biomass of substrates containing only endolithic algae with substrates inhabited by both

epilithic and endolithic algae suggests that only a small proportion of the biomass in and on coral limestone is contributed by the epilithic filamentous algae. In order to investigate further the quantitative role of the endolithic and the epilithic filamentous algae, 2 surveying experiments were carried out.

When the filamentous algae were scraped off a piece of limestone (from 12 m depth) containing endolithic algae, the remaining limestone still contained a considerable amount of chlorophyll a: $9.9 \mu\text{g cm}^{-2}$ in the upper 1.2 cm (compare Table 3); no measurable amount in the remaining 0.8 cm.

Table 5 presents the results of chlorophyll a and dry weight measurements of filamentous algae on a PVC plate from 22 m depth. Only $1.0 \mu\text{g}$ chlorophyll a, or 2.7 mg dry weight cm⁻² were present. These values must be doubled in order to correct for percentage cover.

Table 5. Species composition, percentage cover, chlorophyll a content and dry weight of filamentous algae on a PVC plate. Depth: 22 m

Species composition	Percentage cover	Chlorophyll a ($\mu\text{g cm}^{-2}$)	Dry weight (mg cm ⁻²)
<i>Lyngbya</i> sp.			
<i>Polysiphonia</i> sp.			
<i>Spermothamnion</i> sp.	50	1.0	2.7
<i>Ectocarpus</i> sp.			
<i>Cladophora</i> sp.			

DISCUSSION

When measuring biomass of benthic algae in coral reefs a problem is how to separate the algae from their

Table 4. Results of dry weight determinations for different vegetation components at 12 m and 25 m depth. Dry weight expressed in mg cm⁻² of substrate surface $\pm 95\%$ confidence interval ($\pm t \cdot \frac{S}{\sqrt{n}}$); n: number of samples

Vegetation component	n	12 m			n	25 m		
		Mean area of samples (cm ²)	Mean %-cover of samples	Dry weight (mg cm ⁻²)		Mean area of samples (cm ²)	Mean %-cover of samples	Dry weight (mg cm ⁻²)
1 <i>Archaeolithothamnion dimotum</i>	—	—	—	—	16	44	100	21.8 ± 6.6
2 <i>Hydrolithon boergesenii</i>	8	50	93	13.9 ± 7.5	9	21	96	13.3 ± 6.8
3 <i>Lithophyllum cf. intermedium</i>	8	42	93	12.7 ± 6.7	—	—	—	—
4 Endolithic algae	5	61	98	13.2 ± 9.3	9	34	100	23.2 ± 6.2
5 Epilithic filamentous algae (with <i>Lithophyllum cf. intermedium</i>) on substrates containing endolithic algae	17	76	104	15.2 ± 6.3	20	30	94	25.7 ± 6.0

substrates. While larger filamentous algae may be harvested, although care must be taken not to include limestone scrapings in the algal samples, small filamentous algae and crustose corallines, both common in the reef of Curaçao, required 2 other methods. Chlorophyll *a* measurements were carried out by grinding whole samples including the limestone substrate. Dry weights were determined by oxidizing all organic material present in the sample by means of wet combustion with hydrogenperoxide and taking the weight loss caused by this process as the dry weight of the sample. Of course, both methods measure biomass of endolithic algae plus that of epilithic algae. An impression of the contribution of the epilithic algae can be obtained by comparing the biomass of substrates with and without epilithic algae. Dry weights determined by means of wet combustion include organic matter belonging to dead algal material. However, since all the organic material can essentially be regarded as a food source for herbivores, these data are useful in quantitative studies concerning the role of algae in coral reefs.

So far, few measurements on algae biomass in coral reefs have been carried out. Biomass of filamentous algae harvested from their substrates was measured as chlorophyll *a* (Wanders, 1976a, 1977), as dry weight (Vine, 1974; Wanders, 1976a, 1977) and as wet weight (Brawley and Adey, 1977). Biomass of crustose corallines was mostly measured on an area basis – for instance as cover, relative density or frequency (Litter, 1971, 1973); only Wanders (1976a, 1977) determined chlorophyll *a* in addition. Biomass measurements of endolithic algae are so far lacking.

The chlorophyll *a* data presented in this paper can best be compared with those found by Wanders (1976a) for the shallow reef (0.5 m–3 m depth) of Curaçao. He found that chlorophyll *a* values of the different crustose corallines ranged from 13.4 to 24.3 (mean 17.0) $\mu\text{g cm}^{-2}$. This is higher than the values we found both at 12 m (8.7–11.8 $\mu\text{g cm}^{-2}$) and at 25 m (8.9–11.0 $\mu\text{g cm}^{-2}$). Chlorophyll *a* contents of Wanders' 'sparse turf vegetation' (11.1 $\mu\text{g cm}^{-2}$) and 'dense turf vegetation' (17.9 $\mu\text{g cm}^{-2}$) may be compared with those in our vegetation components 4 and 5: 'endolithic algae' (12.3 $\mu\text{g cm}^{-2}$ at 12 m and 15.6 $\mu\text{g cm}^{-2}$ at 25 m) and 'epilithic filamentous algae on substrates containing endolithic algae' (14.0 $\mu\text{g cm}^{-2}$ at 12 m and 20.5 $\mu\text{g cm}^{-2}$ at 25 m). At greater depths the chlorophyll *a* contents of these vegetations seem to be somewhat higher.

The dry weight values presented here can be compared with data from Vine (1974), Wanders (1976a) and Vooren (1981). Only Vooren (1981) used the same method to determine dry weights, i.e. by means of wet combustion. For comparable vegetation components and depths Vooren's values lie somewhat higher than

ours. This is probably due to the loss of sediment from the samples during the wet combustion process which has been corrected for in this paper and not by Vooren. Very low dry weight values were found by Vine (1974), who compared growth of green filamentous algae in and outside territories of *Pomacentrus lividus* Bl. Schr. and *Acanthurus sohol* Forskal on protected and unprotected settlement plates in a patch reef in the Sudanese Red Sea. For unprotected plates outside territories he found 0.67 mg cm^{-2} at 12 m and 0.09 mg cm^{-2} at 20 m depth (data from his Fig. 2). This is very low in comparison to the 2.7 mg cm^{-2} found on the PVC plate from 22 m in the reef of Curaçao. However, Vine's settlement plates had been in situ for only 30 days in contrast to the PVC plate, which had been in the reef for about 5 years. For plates protected against grazing, Vine (1974) found at 20 m about the same dry weights as for unprotected plates; at 12 m, 8.0 mg cm^{-2} . In the shallow reef of Curaçao dry weight values can be much higher. Wanders (1976a) found 25.5 mg cm^{-2} for dense vegetations of turf algae separated from their substrates. These dense vegetations are found in places not easily accessible to herbivores (Wanders, 1976a).

In summary, it may be concluded that the chlorophyll *a* values and the dry weight values presented in this paper lie well within the range found for these parameters in comparable habitats by other authors. Both chlorophyll *a* and dry weight are useful biomass parameters for benthic algae in coral reefs. Dry weight measurements can be carried out more easily, but chlorophyll *a* measurements seem to be more accurate in view of the narrower confidence intervals.

Comparison of the biomass of the various vegetation components shows that endolithic algae are quantitatively much more important than the epilithic filamentous algae. At 12 m and at 25 m depth, vegetations with and without epilithic filamentous algae do not differ significantly in chlorophyll *a* contents and dry weights. These results are further supported by the observation that a considerable amount of chlorophyll *a* (9.9 $\mu\text{g cm}^{-2}$) can be measured in a piece of limestone substrate from which the epilithic filamentous algae have been scraped off. Also the small amount of biomass found for filamentous algae growing on a PVC plate supports the conclusion that endolithic algae are quantitatively much more important. Probably the same conclusion holds true for the shallow reef (Wanders, 1976a). The differences in chlorophyll *a* content between the 'dense turf vegetation' and the 'sparse turf vegetation' are small – the latter vegetation still contains about 65 % of the biomass of the former. This can probably be attributed to endolithic algae. Possibly, endolithic algae play an important role as food source for herbivores.

Fig. 2 combines the chlorophyll *a* and dry weight values presented in this paper with production data measured by Vooren (1981). The values presented are expressed per unit of substrate surface area for each of the studied vegetation components. For all 3 vegetation components (crustose corallines, endolithic algae, and epilithic filamentous algae on substrates containing endolithic algae) production is lowest at 25 m. This is attributed to the fact that at this depth less light is available for photosynthesis (Vooren, 1981). Despite this, biomass relative to production is high at 25 m. It would seem that at 12 m the high production should be capable of establishing a large standing crop of algae. The absence of such crop suggests heavy grazing pressure; this is in agreement with the observation that at this depth (the 'drop off community') the reef is inhabited by many herbivores. Although the biomass of vegetations with epilithic filamentous algae is hardly higher than that of vegetations without epilithic filamentous algae, production of the former is much higher. Apparently, grazing pressure is heaviest on filamentous algae. This is probably caused by their easy accessibility to herbivores.

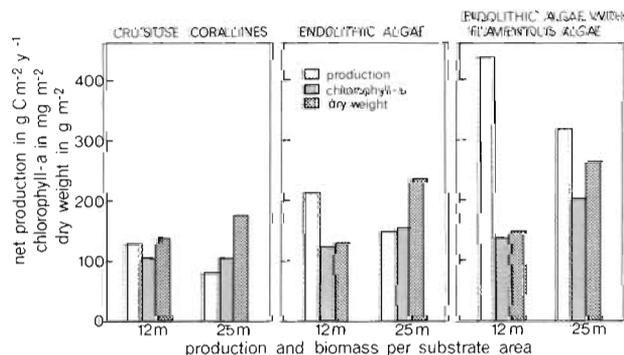


Fig. 2. Net production ($\text{g C m}^{-2} \text{y}^{-1}$) and biomass ($\text{mg chlorophyll } a \text{ m}^{-2}$ and $\text{g dry weight m}^{-2}$) per substrate area covered by the various vegetation components at 12 m and 25 m depth; summary of production data by Vooren (1981) (his Table IV) and chlorophyll *a* and dry weight values from this paper (Tables 3 and 4). 12 m: production for *Hydrolithon boergesenii* calculated from Fig. 3 in Vooren (1981), assuming that in situ light is about 50 % of available light; mean biomass values for *H. boergesenii* and *Lithophyllum cf. intermedium*. 25 m: mean production and biomass values for *Archaeolithothamnion dimotum* and *H. boergesenii*

In Fig. 3 data on biomass and production are expressed per m^2 of reef surface area and summarized for the different reef zones. For this purpose biomass data from this paper and production data from Vooren (1981) were combined with data on relative coverage of the various vegetation components as measured by de Groot and de Ruyter van Steveninck (unpubl.). These authors measured relative coverage in 2 line

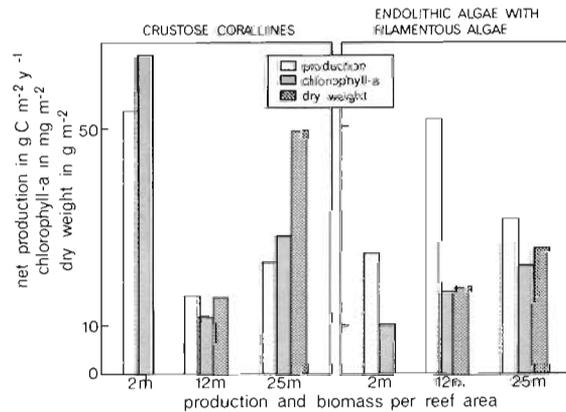


Fig. 3. Net production ($\text{g C m}^{-2} \text{y}^{-1}$) and biomass ($\text{mg chlorophyll } a \text{ m}^{-2}$ and $\text{g dry weight m}^{-2}$) per reef surface area for various vegetation components at 3 different depths; data in Fig. 2 are combined with relative coverages of the vegetation components calculated from Table IV in Wanders (1976a) for 2 (0.5–3) m and from data presented in Table 6 (this paper) for 12 m and 25 m. For 2 (0.5–3) m production was calculated from Table IX in Wanders (1976a) and chlorophyll *a* values were taken from Table VII in Wanders (1976a)

transects at about 12 m and 25 m depth (Table 6). Their Transect I corresponds with the area investigated in this paper and the values for this transect have been used. Table 6 shows that relative coverages do not vary greatly for these 2 transects on the reef. For the shallow reef, data have been calculated from Wanders (1976a). Damsel fish territories and vegetations consisting of endolithic algae only have been left out of Fig. 3, because their percentage cover in the reef is low (Table 6). Coral rubble and sand are quantitatively important components in the reef, especially at 12 m

Table 6. Percentage cover per total reef surface of substrates potentially inhabited by algae in 2 line transects in the reef of Curaçao as measured by de Groot and de Ruyter van Steveninck (unpubl.) at about 12 m and 25 m depth. Mean values from measurements perpendicular and parallel to the coastline

Vegetation component	Transect I		Transect II	
	12 m	25 m	12 m	25 m
Crustose corallines (Veg. comp. 1, 2 and 3)	12	29	14	25
Endolithic algae (Veg. comp. 4)	3	<1	<1	1
Epilithic filamentous algae on substrates containing endolithic algae (Veg. comp. 5)	12	10	12	7
Damsel fish territories	2	<1	1	–
Rubble and sand	25	25	32	17

(Table 6) but since biomass data on these substrates are lacking they have not been included in Fig. 3.

For crustose corallines, biomass and production are highest at 2 (0.5–3) m and lowest at 12 m. This is mainly caused by the coverage of these algae at various depths: 38 %, 12 % and 29 % at 2 (0.5–3) m, 12 m and 25 m respectively. For vegetations with epilithic filamentous algae, production and chlorophyll *a* values are lowest in the shallow reef due to low production and biomass per covered substrate as well as low percentage cover in the reef (9 %). Highest biomass was found at 25 m while production was highest at 12 m. Since relative coverage of this vegetation component was the same at both depths (12 %) these differences must be attributed to differences in biomass and production of the sampled vegetations. In view of the rather high relative coverage of coral rubble and sand, especially at 12 m, both substrates probably inhabited by endolithic algae, the quantitative role of endolithic algae in the reef as a whole may be more important than indicated in the above survey.

In summary, it may be concluded that the hypothesis, raised by van den Hoek et al. (1978), that grazing pressure is highest in the 'drop off community' and decreases at greater depths is now supported by quantitative data. Grazing pressure is highest on the filamentous algae and less on the crustose corallines and the endolithic algae. Van den Hoek et al. (1978) observed that coverage of crustose corallines is lowest in the 'drop off community' and it has now been shown that biomass per area of reef surface covered by these algae is also lowest in this community (12 m). Biomass of vegetations with epilithic filamentous algae is indeed higher in the 'roof shingle community' (25 m) than in the 'drop of community' as observed by van den Hoek et al. (1978). It will be interesting to extend measurements on biomass and production to reef zones deeper than 25 m. There the reef is dominated by a vegetation of fleshy and filamentous algae (van den Hoek et al., 1978: 'deep algal community', Fig. 1). It would further be interesting to compare the 'drop off community', the 'roof shingle community' and the 'deep algal community' for grazing pressure in experiments in which substrates are excluded from grazing (Wanders, 1977). The important role of endolithic algae in total biomass has now been demonstrated. It will be useful to further investigate their importance as a food source for herbivores and to estimate the amount in which they are present in different substrates such as living corals and crustose corallines, coral rubble and sand, and to investigate their possible destructive effects on the stability of the reef structure.

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LITERATURE CITED

- Adey, W. H., Vassar, J. M. (1975). Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). *Phycologia* 14: 55–69
- Bak, R. P. M. (1976). The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Neth. J. Sea Res.* 10: 285–337
- Bak, R. P. M., van Eys, G. (1975). Predation of the sea urchin *Diadema antillarum* Philippi on living coral. *Oecologia* Berl. 20: 111–115
- Bakus, G. J. (1966). Some relationships of fishes to benthic organisms on coral reefs. *Nature, Lond.* 210: 280–284
- Bakus, G. J. (1967). The feeding habits of fishes and primary production at Eniwetok, Marshall Islands. *Micronesia* 3: 135–149
- Brawley, S. H., Adey, W. H. (1977). Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. *Env. Biol. Fish.* 2: 45–51
- Brock, R. E. (1979). An experimental study on the effect of grazing by parrotfishes and role of refuges in benthic community structure. *Mar. Biol.* 51: 381–388
- Dart, J. K. G. (1972). Echinoids, algal lawn and coral recolonization. *Nature, Lond.* 239: 50–51
- Day, R. W. (1977). Two contrasting effects of predation on species richness in coral reef habitats. *Mar. Biol.* 44: 1–5
- Earle, S. A. (1972). The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. In: Colette, B. B., Earle, S. A. (eds.) *Results of the Tektite program: Ecology of coral reef fishes*. Natural History Museum, Los Angeles County, Science Bulletin 14: 17–44
- Hiatt, R. W., Strasburg, D. W. (1960). Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* 30: 65–127
- Hoek, C., van den (1969). Algal vegetation-types along the open coasts of Curaçao, Netherlands Antilles. *Proc. K. Ned. Acad. Wet. (Ser. C)* 72: 537–577
- Hoek, C., van den, Breeman, A. M., Bak, R. P. M., Buurt, G., van (1978). The distribution of algae, corals and gorgonians in relation to depth, light attenuation, water movement and grazing pressure in the fringing coral reef of Curaçao, Netherlands Antilles. *Aquat. Bot.* 5: 1–46
- Hoek, C., van den, Cortel-Breeman, A. M., Wanders, J. B. W. (1975). Algal zonation in the fringing coral reef of Curaçao, Netherlands Antilles, in relation to zonation of corals and gorgonians. *Aquat. Bot.* 2: 235–270
- Lewis, J. B. (1977). Processes of organic production on coral reefs. *Biol. Rev.* 52: 305–347
- Littler, M. M. (1971). Standing stock measurements of crustose coralline algae (Rhodophyta) and other saxicolous organisms. *J. exp. mar. Biol. Ecol.* 6: 91–99
- Littler, M. M. (1973). The population and community structure of Hawaiian fringing-reef crustose corallinaceae (Rhodophyta, Cryptonemiales). *J. exp. mar. Biol. Ecol.* 11: 103–120

- Lorenzen, C. (1967). Determination of chlorophyll and phaeopigments: spectrophotometer equation. *Limnol. Oceanogr.* 12: 343-346
- Marsh, J. A. (1970). Primary productivity of reef-building calcareous red algae. *Ecology* 5: 255-263
- Ogden, J. C. (1976). Some aspects of herbivore plant relationships on Caribbean reefs and seagrass beds. *Aquat. Bot.* 2: 103-116
- Ogden, J. C., Brown, R. A., Salesky, N. (1973). Grazing by the echinoid *Diadema antillarum* Philippi: Formation of halos around West Indian patch reefs. *Science, N. Y.* 182: 715-717
- Ogden, J. C., Lobel, P. S. (1978). The role of herbivorous fishes and urchins in coral reef communities. *Envir. Biol. Fish.* 3: 49-63
- Randall, J. E. (1961). Overgrazing of algae by herbivorous marine fishes. *Ecology* 42: 812
- Vine, P. J. (1974). Effects of algal grazing and aggressive behaviour on the fishes *Pomacentrus lividus* and *Acanthurus sohol* on coral reef ecology. *Mar. Biol.* 24: 131-136
- Vollenweider, R. A. (1969). A manual on methods for measuring primary production in aquatic environments, Blackwell, Oxford
- Vooren, C. M. (1981). Photosynthetic rates of benthic algae from the deep coral reef of Curaçao. *Aquat. Bot.* 10: 143-154
- Wanders, J. B. W. (1976a). The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). I: Primary productivity in the coral reef. *Aquat. Bot.* 2: 235-270
- Wanders, J. B. W. (1976b). The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). II: Primary productivity of the *Sargassum* beds on the north-east coast submarine plateau. *Aquat. Bot.* 2: 327-335
- Wanders, J. B. W. (1977). The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). III: The significance of grazing. *Aquat. Bot.* 3: 357-390

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