Biomass and production of two *Halimeda* species in the Southwest New Caledonian lagoon

Halimeda
Production
Phytobenthos
New Caledonia
Biomass

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Phytobenthos
Nouvelle-Calédonie
Biomasse

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ABSTRACT

Two algal communities on unconsolidated sand, dominated by two *Caulerpa* populations,were studied in the southwestern New Caledonian lagoon. Biomass, growth rates and production were measured at two stations over one year.

Biomass and growth rate of *Halimeda* were estimated monthly by counting the number of new and lost segments on tagged plants and by weighing them.

Production was assessed monthly by comparing two successive measurements. The average rates measured were 0.60 s f^{-1} d^{-1} (segment frond^{-1} day^{-1}) for *Halimeda incrassata* and 0.15 s f^{-1} d^{-1} for *H. discoidea*. Production in terms of organic carbon amounted to 3.79 g m^{-2} y^{-1} for *H. incrassata* and 3.37 g m^{-2} y^{-1} for *H. discoidea*. The production of *H. discoidea* population is subject to seasonal variations.

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RÉSUMÉ

Biomasse et production de deux espèces d'*Halimeda* dans le lagon sud-ouest de Nouvelle-Calédonie

La biomasse, le taux de croissance et la production ont été étudiés sur deux populations de Caulerpales vivant sur les fonds meubles du lagon sud-ouest de Nouvelle-Calédonie.

Le taux de croissance a été calculé tous les mois pendant un an, grace à une méthode directe qui consiste à compter et à peser le nombre d'articles apparus et disparus sur des plantes étiquetées. La comparaison de deux relevés successifs permet d'obtenir une estimation de la production.

L'accroissement moyen est de 0,60 articles par jour par fronde pour *Halimeda incrassata* et de 0,15 articles par jour par fronde pour *H. discoidea*. La production exprimée en carbone organique est de 3,79 g m^{-2} an^{-1} pour *H. incrassata* et de 3,37 g m^{-2} an^{-1} pour *H. discoidea*. La production de la population d'*H. discoidea* est soumise à des variations saisonnières.

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INTRODUCTION

The calcareous green algal genus *Halimeda* (Caulerpales, Halimedaceae) is recognized as a major element of tropical reefs (Hillis-Colinvaux, 1980) on both hard and soft substrata. It is encountered in the intertidal zone but extends to deep reef slopes (Littler *et al.*, 1985). The first study on *Halimeda* growth was presented by Colinvaux *et al.* (1965) following laboratory observations. Several authors have since worked on *Halimeda* growth, production and calcification. A direct method using the *Halimeda* thalli structure, composed of associated segments, consists in the count of incremental segments, either from tagged fronds (Meinesz, 1980; Drew, 1983; Drew and Abel, 1983 and 1985; Abel and Drew, 1985) or from fronds marked with a chemical such as Alizarin Red-S (Wefer, 1980; Multer, 1988; Payri, 1988). Physiological methods involving, for example, photosynthetic oxygen measurements (Buesa, 1977; Morrissey, 1985; Littler *et al.*, 1983; Payri, 1988) or alkalinity measurements (Payri, 1988) can also be used. In the present study, the direct method on tagged fronds is applied.

In New Caledonia *Halimeda* has been studied during floristic inventories (Garrigue, 1985; Garrigue and Tsuda, 1988) but up to now no data on growth, organic and inorganic production have been available. To fill this gap, the present study was designed to determine the composition of Caulerpales assemblages, the biomass of the various species, the growth and loss rates and the annual production and senescence of two populations of *Halimeda* species.

MATERIALS AND METHODS

The study, conducted on two stations located in front of Noumea (Fig. 1), concerned two populations of mixed Caulerpale.

Station 1 was located in the internal lagoon, in Sainte-Marie Bay at a depth of 11 m where the substratum was coarse coral and shell sand. Station 2 was in the external part of the lagoon, on the reef shelf close to Snark Banks at a depth of 24 m. The substratum was coarse sand.

Biomass assessment method

At each station, a rope was used to delimit a permanent 40 x 40 m quadrat (1 600 m^2). Sampling was carried out approximately each month, from December 1983 to November 1984. Twenty samples per month were taken from random placed stainless steel 1 x 1m quadrats. All the macrophytobenthos present in half of the quadrat was collected and placed in numbered plastic bags. A total surface of 120 m^2 was collected in twelve months, which represents 7.5 % of the whole surface of sampling area.

At the laboratory, the algae were cleaned of epiphytes and the rhizoids removed. The algae were then dried to a constant weight at 60°C and weighed for dry weight (dw) determination (Crisp, 1971).

Calcification was found for all the *Halimeda* species by dissolving some samples in 0.1N HCl. It is expressed as a percentage of the dry weight.

In order to transform dry weights to organic matter (ash free dry weight: afdw), the following biometric relations (Garrigue and Di Matteo, 1991) were used:

- for *H. incrassata* : afdw = - 0.039 + 0.215 dw,
- for *H. discoidea* : afdw = 0.079 + 0.422 dw.

To approximate the organic carbon content from *Halimeda* the following conversion coefficient has been adopted : 1 g afdw = 0. 40g C (Steele, 1974).

Production study method

The *Halimeda* genus grows by development of new segments at the extremities of the axes; the segment emergence rate can be used to evaluate frond growth. To calculate productivity, a direct method was used in which the growth observed on tagged plants was cumulated on a 1 x 1 m quadrat, divided into 100 squares (10 x 10 cm), fixed at the

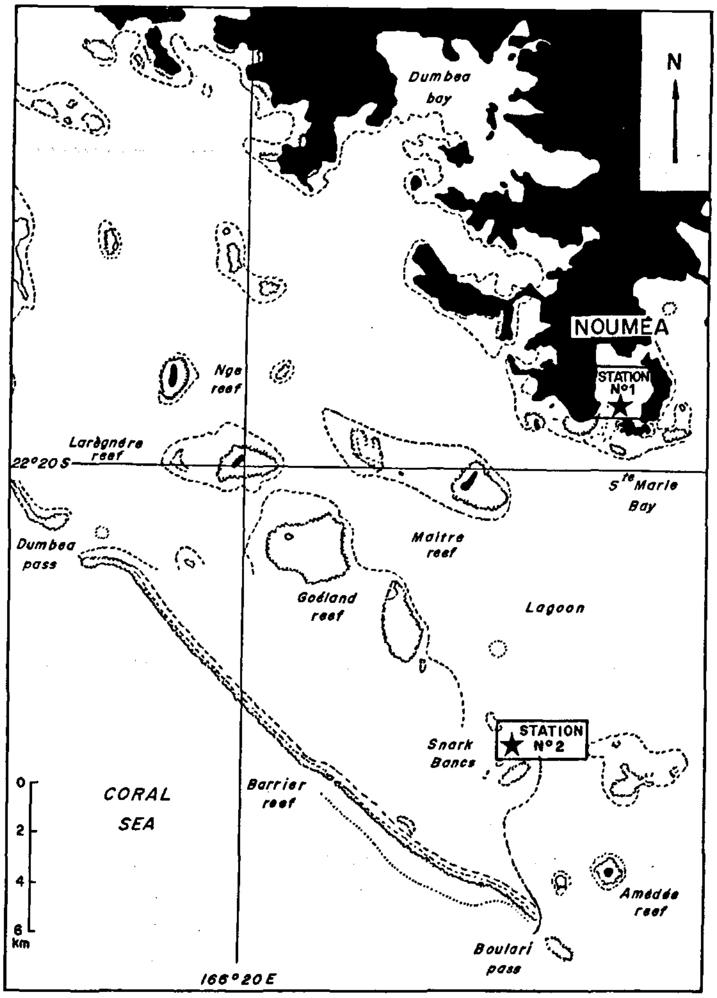

Figure 1

Location of the stations studied.

Localisation des stations étudiées.

Table 1

Species composition of the stations (relative frequency of the frond for each species of Halimeda*; + = species present).*

Composition spécifique des stations (la fréquence relative des frondes pour chaque espèce d'*Halimeda* est exprimée en pourcentage; + = espèce présente).

Species	Station 1	Station 2
Halimeda cylindracea Decaisne		5%
Halimeda discoidea Decaisne		77%
Halimeda incrassata Ellis (Lamouroux)	90%	5%
Halimeda macroloba Decaisne	10%	11%
Halimeda macrophysa Askenasy		+
Halimeda simulans Howe		6%
Caulerpa bikinensis Taylor		+
Caulerpa cupressoides (West) C.Agardh	+	+
Caulerpa okamurai Weber van Bosse		+
Caulerpa racemosa *var.corynephora* (Mont.) Weber van Bosse		+
Caulerpa sertularioides (Gmelin) C.Agardh		+
Caulerpa taxifolia (Vahl) C.Agardh		+

centre of each station. At each survey, the total number of fronds in the quadrat was counted as well as the number of fronds with gains or losses of segments; the new fronds were noted and tagged. The number of new and lost segments was calculated for each time lapse separating two sampling periods. Thus it was possible to obtain the mean number of segments/frond/day, this value representing the increase or decrease rate between two surveys. By comparing two successive measurements, the mean frond evolution and senescence were assessed. As the measures were not done on a daily basis, true segment loss or even gain could have been overlooked.

In order to express the calculated production in g dry weight m^{-2} $year^{-1}$ (gdw m^{-2} y^{-1}), the biometric relation between the number of segments and the dry weight was evaluated by a linear regression for the two *Halimeda* species.

RESULTS

Species composition

Six species of *Halimeda* and six species of *Caulerpa* were collected on the two stations studied. The *Halimeda* species were identified with the keys from Hillis-Colinvaux (1980). Voucher specimens are held in the ORSTOM Oceanography Laboratory of Noumea (Garrigue and Tsuda, 1988). Table 1 shows the species composition of the two stations and the percentage of *Halimeda* fronds. Station 2 supports the greatest species richness with six species of *Halimeda* and six species of *Caulerpa*. *H. discoidea* dominates the assemblage, this species being found mainly with *H. macroloba*. The species richness of station 1 is very low, *H. incrassata* dominating the vegetal assemblage, which is homogenous.

Biomass distribution

Station 1 presents the highest mean biomass with 20.60 gdw m^{-2}. About a quarter of this biomass is composed of organic matter (4.91 gafdw m^{-2}). $CaCO_3$, which may pass directly into the sediment when the *Halimeda* segments break down, accounts for 68 % of the dry weight. *H. incrassata* dominates the assemblage in frond number (950 fronds collected) as well as in biomass.

This species is responsible for the bulk of the dry weight (81 %) and nearly all the $CaCO_3$ (86 %) on this station (Fig. 2); but it only contributes to 72 % of the total organic matter, the remaining being provided mostly by *Caulerpa cupressoides* (20 %).

The dry weight biomass at station 2 is 15.85 gdw m^{-2} . Here, also, about a quarter of the biomass is composed of organic matter (4.47 gafdw m^{-2}), and 68 % of the dry weight is accounted for by $CaCO_3$. *Halimeda discoidea* dominates the assemblage in frond number (77 %) whereas in dry weight biomass, *H. macroloba* is the most important species (35 %), followed by *H. discoidea* (30 %). Despite its important frond number, the *H. discoidea* dry weight biomass is slightly lower than that of *H. macroloba* with respectively 4.66 and 5.59 gdw m^{-2} ; this is mainly due to the morphology of *H. macroloba* the fronds of which contain a great number of large-size segments with calcification constituting 84 % of the dry weight of the plant. *H. incrassata* represents only 11 % of the dry weight biomass. In term of organic matter biomass *H. discoidea* which accounts for the greatest portion (42 %), is followed by *Caulerpa* spp., all species combined (25 %).

Potential production of two *Halimeda* populations

Biometric relations

For *Halimeda discoidea* of station 2, the biometric relation between the number of segments (S) and the dry weight (dw in g) is expressed as:

$dw = 0.032\ S - 0.068$,
$r = 0.88$,
$n = 1960$,
r = correlation coefficient, n = sample size

For the *Halimeda incrassata* population of station 1, the relation linking the number of segments (S) to the dry weight (dw in g) is established as follows :

$dw = 0.023\ S + 0.260$,
$r = 0.84$,
$n = 1216$,
r = correlation coefficient, n = sample size

In Tables 2 and 3, frond density, increase and decrease rates, production and plant matter loss are presented.

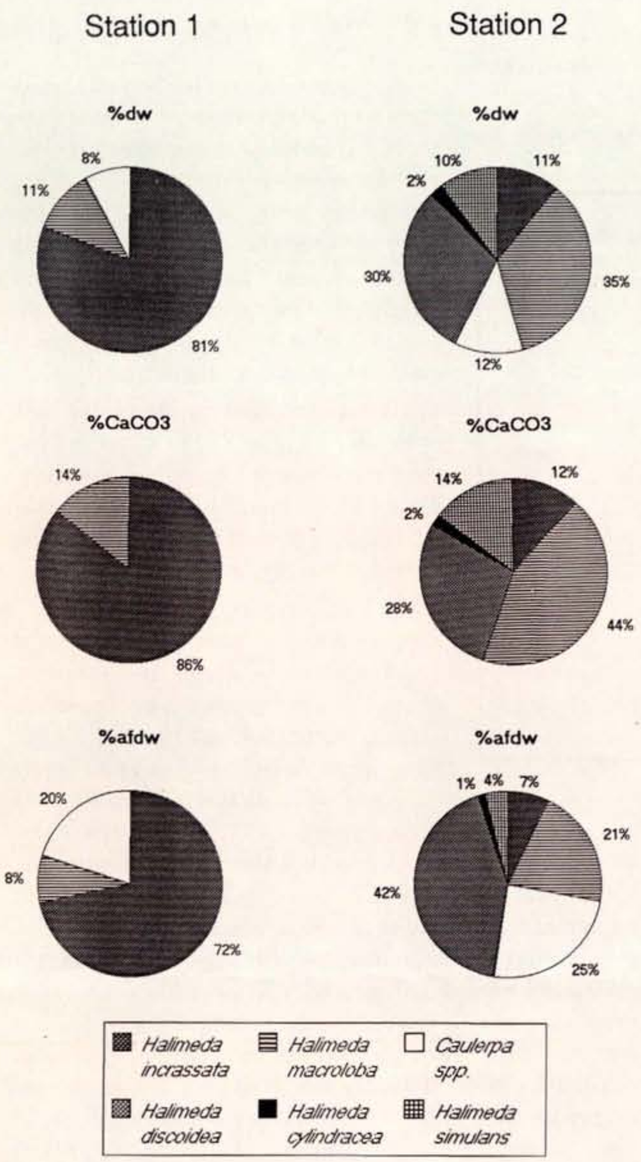

Figure 2

Biomass distribution in the stations in dry weight (%), in calcium carbonate (%), in ash-free dry weight (%).

Distribution des biomasses en poids sec (%), en carbonate de calcium (%), en poids sec décalcifié (%).

By adding the dry weight production and loss of *Halimeda discoidea* (Tab. 2), the annual production and the plant material released in the environment are estimated (Tab.4). The mean monthly increase rate, for one year, is 0.15 segment per frond per day, which enables us to deduce an annual production of 21.26 gdw m^{-2} y^{-1}, a value close to that stated in Table 4. The mean monthly decrease rate, for one year, is also 0.15 segment/frond/day. So the annual production and senescence seem to be in balance.

Calcification measures show that 65 % of the dry weight is composed of calcium carbonate. This permits the calculation of calcium carbonate production and loss (Tab. 4).

After adding the quantities of dry weight produced by *Halimeda incrassata* between each survey (Tab. 3), the deduced production value is 42.93 gdw m^{-2} during the 354 days of experimentation. This is expressed on a yearly basis in Table 4. The calculated daily increase rate amounts to 0.60 segments per frond per day. This last value permits calculation of the annual production at 40.56 gdw m^{-2} y^{-1}, which is slightly lower than the value obtained from the direct observation surveys. The same operations were undertaken for plant senescence. Dry weight released is 41.45 gdw m^{-2} for 354 days, which in turn corresponds to an annual loss of 42.74 gdw m^{-2} (Tab. 4). Calcification represents 72 % of the dry weight.

Seasonal effect

Table 2 suggests that the increase and decrease rates of *Halimeda discoidea* are not uniform throughout the year. In order to test a possible seasonal effect, a one-way variance analysis is conducted on log transformed data. Table 5 shows that there are significant differences between the months in the increase and decrease rates ($\alpha = 0.05$). A Newman and Keuls test, modified by Kramer (1956) for the application to unequal numbers of replications, indicates that months can be grouped into two periods: November to April and June to October (rates not different within groups at $\alpha = 0.05$).

A similar one-way variance analysis for *Halimeda incrassata* (Tab. 5) indicates that there is no significant difference between months for the increase rate; but in contrast there are significant differences between months for the decrease rates ($\alpha = 0.05$).

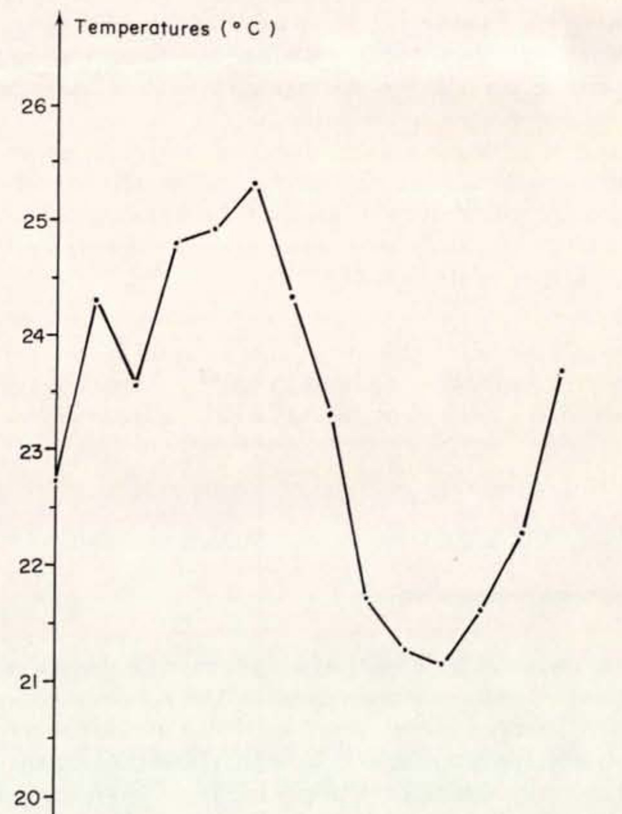

Figure 3

Water temperature measured during the experiment.

Température de l'eau mesurée pendant l'expérience.

Table 2

Halimeda discoidea. *Frond density, increase and decrease rate, production and plant matter loss for the population at station 2.*

Halimeda discoidea. Densité, taux de croissance et de décroissance, production et perte de matière pour la population de la station 2.

Year **Date of measure**	1983 11/7	1983 12/12	1984 1/5	1984 2/1	1984 3/20	1984 4/10	1984 5/10	1984 5/28	1984 8/13	1984 9/7	1984 10/12	1984 11/5
Time interval between consecutives measures in days		35	24	27	48	21	30	18	77	25	35	24
Frond density fronds m^{-2}		7.8	14.0	15.6	9.0	14.4	13.2	12.2	25.0	8.4	6.8	9.2
Increase rate segments f^{-1} d^{-1}		0.14	0.25	0.22	0.13	0.20	0.13	0.13	0.08	0.12	0.07	0.17
Production (g dry weight m^{-2})		1.17	2.66	2.94	1.75	1.89	1.60	0.86	4.93	0.75	0.47	1.15
Decrease rate segments f^{-1} d^{-1}		0.10	0.16	0.22	0.16	0.12	0.18	0.20	0.08	0.17	0.12	0.15
Loss of plant matter (g dry weight m^{-2})		0.91	0.90	2.63	3.82	0.67	2.46	1.47	2.27	3.38	1.08	0.73

Table 3

Halimeda incrassata. *Frond density, increase and decrease rate, production and plant matter loss of the population at station 1.*

Halimeda incrassata. Densité, taux de croissance et de décroissance, production et perte de matière pour la population de la station 1.

Year **Date of measure**	1983 11/20	1983 12/4	1984 1/9	1984 2/6	1984 3/22	1984 4/12	1984 5/30	1984 8/8	1984 9/5	1984 10/9	1984 11/8
Time interval between consecutives measures in days		24	26	28	45	21	48	70	28	34	30
Frond density fronds m^{-2}		10.1	8.5	6.7	6.3	6.8	6.7	13.6	4.0	6.4	4.5
Increase rate segments f^{-1} d^{-1}		0.42	1.06	0.26	0.25	0.48	0.72	0.69	0.31	0.67	1.19
Production (g dry weight m^{-2})		2.60	5.65	1.38	1.89	1.84	5.58	15.37	1.06	3.61	3.95
Decrease rate segments f^{-1} d^{-1}		1.16	0.98	1.2	0.47	0.34	0.55	0.09	0.66	0.88	1.22
Loss of plant matter (g dry weight m^{-2})		3.91	6.18	6.83	3.52	1.29	4.39	1.23	6.04	3.01	5.65

Table 4

Production and loss estimated for the H.discoidea *and* H.incrassata *populations.*

Production et perte de matière pour les populations d'*H.discoidea* et *d'H.incrassata.*

Species	Parameters expressed in g m^{-2} $year^{-1}$	Production	Loss	P/B
Halimeda discoidea	Dry weight	20.17	20.32	4.33
	$CaCO_3$	13.11	13.21	
	Organic matter	8.43	8.50	
	Organic carbon	3.37	3.40	
Halimeda incrassata	Dry weight	44.26	42.74	2.57
	$CaCO_3$	31.87	29.20	
	Organic matter	9.48	9.15	
	Organic carbon	3.79	3.66	

Table 5

Results of the one-way analysis of variance (for $\alpha = 0.05$, NS : no significant, + : significant).

Source of variability	Degree of freedom	Sum of square	Mean square	F
Halimeda discoidea production				
between group	10	30.43	3.04	
residual	272	161.11	0.59	5.14 +
total	282	191.54		
Halimeda discoidea senescence				
between group	10	14.20	1.42	
residual	132	81.82	0.62	2.29 +
total	142	96.01		
Halimeda incrassata production				
between group	9	16.52	1.84	
residual	58	74.58	1.29	1.43NS
total	67	91.09		
Halimeda incrassata senescence				
between group	9	24.13	2.68	
residual	59	59.13	1.00	2.68 +
total	68	83.27		

DISCUSSION

Seasonal effect

A seasonal effect in the production cycle of *Halimeda discoidea* may exist. Two distinct periods have been recognized. During the first period (November to April), the measured increase rate is the highest. This period corresponds to the southern hemisphere summer. The second period (May to October), during which the lowest increase rates are observed corresponds to the winter in the southern hemisphere. The increase rate appears to be associated with the water temperature which is at its highest in summer, reaching 25°5C, whilst during the winter it drops to 19°C (Fig. 3). A temperature of 23°C seems to be a limit below which *H. discoidea* growth is slowed down. For this reason May and October, during which the temperature drops to or below 23°C, are turning points for the growth of this species (Fig. 3).

Table 6

Summary of the Halimeda *production studies. (s : segment, f : frond, d : day, y : year)*

Tableau présentant le récapitulatif des études de production d'*Halimeda* citées dans le texte. (s : segment ou article, f : fronde, d : jour, y : année).

AUTHORS	LOCATION	DEPTH	WATER TEMPERATURE	SPECIES	BIOMASS ($g\ m^{-2}$)	GROWTH ($s\ f^{-1}\ d^{-1}$)	ORGANIC CARBON PRODUCTION ($g\ m^{-2}\ y^{-1}$)	P/B
BACH (1979)	Florida	0.95-3.9m	20 to 32°C	*H.incrassata*	5.8			1
DREW (1983)	Great Barrier Reef	1 - 21m	23 to 30°C	*H.opuntia* and *H.copiosa*	500	$s\ d^{-1}$: 0.16	117	
GARRIGUE this work	New caledonia	11m	winter < 23°C summer > 23°C	*H.incrassata*	17.21	0.60	Organic carbon: 3.79 CaCO3 : 31.87	2.57
		24m		*H.discoidea*	4.66	0.15	Organic carbon: 3.37 CaCO3 : 13.11	4.33
MULTER (1988)	Caribbean	1 - 2.5m	27 to 32°C	*H.incrassata* and *H.monile*	$f\ m^{-2}$: 36	1.73	CaCO3 : 97.01	
PAYRI (1988)	French Polynesia	0.5m		*H.incrassata*	7.75	3.3	Organic carbon: 5.8 CaCO3 : 74.5	8
				H.discoidea	2.20		CaCO3 : 14	
WEFER (1980)	Bermuda	1 - 4m	winter < 20°C summer > 20°C	*H.incrassata*	6.7		CaCO3 : 50	7

For *Halimeda* incrassata the estimations were based on fewer data than for the *H. discoidea* population. Thus, a succession of only 38 fronds was observed in the reference quadrat during one year and only 15 new fronds appeared. This is due to the fact that *H. incrassata* fronds have a greater longevity (50 % of the fronds reach 150 days, five months) than *H. discoidea* fronds (50 % of the fronds reach only 90 days, three months; Garrigue, 1985). The significance of production and loss for this species is unknown; consequently we may say no more than that *H. incrassata* population shows a balanced state (production: 44.26 gdw $m^{-2}\ y^{-1}$, loss : 42.74 gdw $m^{-2}\ y^{-1}$, difference : 1.52 gdw $m^{-2}\ y^{-1}$).

Comparison of the two populations studied

The two populations studied originate from different environments. The increase rate and the production of *Halimeda incrassata* are greater than those of *H. discoidea* (Tab. 4). Accordingly, the highest density of *H. discoidea* (12 fronds m^{-2} against 8 fronds m^{-2} for *H. incrassata*) is not sufficient to compensate for the difference between increase rates of the two populations. The dry weight production of *H. discoidea* only represents 45 % of that of the *H. incrassata* population, but in terms of organic matter *H. discoidea* production reaches 89 % of that of *H. incrassata.*

The production/biomass ratio is 4.33 for *Halimeda discoidea* and 2.57 for *H. incrassata*, in dry weight. One may observe that independently of its production, the *H. incrassata* frond population renews itself every five months, which corresponds to the frond longevity determined for this species (Garrigue, 1985). In contrast, the *H. discoidea* population shows a higher productivity which results in turnover shorter than three months. This value coincides with the estimated longevity of 50 % of the fronds calculated as being three months (Garrigue, 1985). Even though productivity is high, biomass stays low because population production is counterbalanced by frond mortality.

Comparison with other results

Table 6 shows a summary of the studies on *Halimeda* populations and their production. The productivity of the populations studied by Drew (1983) on the Great Barrier Reef is the highest of all. There the species are established on a hard substratum (hard bottom species) and present high biomasses of up to 500 gdw m^{-2}, whereas in all the other studies the species grow on soft substrata and show a more individual character with fronds scattered on the substrata and low density and biomass. Despite these differences, it is interesting to note that the growth rates of the Great Barrier Reef populations (0.16 segments d^{-1}) and of the *H. discoidea* population of the present study (0.15 segments d^{-1}) are similar.

Table 6 indicates that for *Halimeda incrassata* the New Caledonian population shows a biomass of 17.21 gdw m^{-2} (8 f^{-1} m^{-2}) which is intermediate between that from the Caribbean 36 f^{-1} m^{-2} (Multer, 1988) and those of the population native to Florida 5.8 gdw m^{-2} (Bach, 1979), Bermuda 6.7 gdw m^{-2} (Wefer, 1980) and Polynesia 7.75 gdw m^{-2} (Payri, 1988). Despite this, the New Caledonian population has the lowest growth rate 0.60 s f^{-1} d^{-1} compared with 3.3 and 1.73 s f^{-1} d^{-1} for the Polynesian and Caribbean populations respectively. In the same way, calcium carbonate production of the New Caledonian population is lower 31.87 g m^{-2} y^{-1} than that of the other populations with 97.01, 74.5, and 50 g m^{-2} y^{-1} respectively for the Caribbean, Polynesian and Bermuda populations. The differences may arise from the alkalinity, staining or tagging methods which have been used. Nevertheless a common point may link Caribbean, Polynesian, Florida and Bermuda populations: they all grow in shallow water at depth of 1 to 4 m whereas the New Caledonian population grows at 11 m.

The New Caledonian population presents an organic carbon production (3.79 g m^{-2} y^{-1}) lower than the Polynesian one (5.8 g m^{-2} y^{-1}) obtained by metabolic measurement.

The production/biomass ratio is of the same order of magnitude for the Polynesian and the Bermuda populations (8 and 7); but is lower for the New Caledonian and Florida populations (2.57 and 1). This indicates that the Polynesian and Bermuda populations present a productivity higher than that of the New Caledonian and Florida populations.

The biomass of the New Caledonian *Halimeda discoidea* population is twice the biomass of the Polynesian one (4.66 and 2.20 gdw m^{-2}). However carbonate production is of the same order of magnitude for the two populations (13.11 and 14 g m^{-2} y^{-1}) despite the great differences between the depths of those two populations, respectively 24 and 0.5 m.

Wefer (1980) remarks that below 20°C, during winter, the *Halimeda incrassata* population presents a decrease in growth rate. Payri (1988) shows that the rate of net primary production is higher in summer than in winter for the populations of *H. opuntia* and *H. incrassata*. The same phenomenon was observed for temperatures below 23°C in New Caledonia for the *H. discoidea* population of station 2. In New Caledonia, the water temperature falls below 23°C during the winter (Garrigue, 1985) which results in slower growth and production rates for *H. discoidea*.

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