Growth rates of the salp
Thalia democratica in Tikehau atoll
(Tuamotu is.)

Robert LE BORGNE (1) and Philippe MOLL (1)

ABSTRACT

Two different and independent methods were used to assess the growth rate of Thalia democratica: *the method of* HERON *and* BENHAM *(1985), which uses population parameters, and the* C:N:P *ratios method, which is based on physiological and chemical measurements. The hourly length increment, produced by the first method, is 25 to 28 ‰, which is equivalent to a hourly weight increment of 53 to 60 %. The second method leads to similarly high weight increase rates of 33 to 36 % per hour. So far, such high values have never been recorded for this species or other zooplanktonic organisms, and could be the result of a high temperature in the lagoon (30 °C) and a great amount of small organic particles that can be filtered by the Salps.*

KEY WORDS : Thaliaceans — Growth — Atolls.

RÉSUMÉ

LE TAUX DE CROISSANCE DE LA SALPE *Thalia democratica* DANS L'ATOLL DE TIKEHAU (TUAMOTU)

Deux méthodes différentes et indépendantes l'une de l'autre, sont utilisées pour déterminer le taux de croissance de T. democratica: *la méthode de* HÉRON *et* BENHAM *(1985), basée sur l'observation de paramètres décrivant la population et la méthode des rapports* C:N:P, *utilisant les mesures de physiologie et de composition élémentaire. Avec la première méthode, la longueur augmente de 25 à 28 ‰ en une heure, ce qui équivaut à une augmentation horaire de poids de 53 à 60 %. La seconde méthode fournit des résultats voisins, quoiqu'un peu plus faibles, pour la croissance pondérale: 33 à 36 %. Ces valeurs sont les plus élevées pour cette espèce et même pour tout organisme zooplanctonique, à l'heure actuelle, et pourraient être dues à la richesse du lagon de l'atoll en particules organiques et à sa température, alors voisine de 30 °C.*

MOTS-CLÉS : Thaliacés — Croissance — Atolls.

INTRODUCTION

Repeated observations on zooplankton were made in the atoll of Tikehau (Tuamotu islands, French Polynesia) between the 30th of March and the 10th of April 1985, and showed high numbers of individuals and dry weights of *Thalia democratica*, a pelagic Tunicate (Salpidae). According to BLANCHOT and MOLL (1986), this species makes 24 % of the indivi- duals of the mesozooplankton (200 μm-2 mm) and 8 % of its dry weight, whereas it stands for 85 % of the numbers and 63 % of the dry weight in the larger size fraction (> 2 mm). Thanks to their asexual reproduction (through budding), the wide spectrum of particles they can feed on, and their high growth rate, Salps can swarm after a phytoplanktonic bloom or the liberation of organic particles by benthic organisms. Such swarms are transient phenomenons,

(1) *Centre ORSTOM, BP A5, Nouméa Cedex, New Caledonia.*

and are worth studying because their consequence on the pelagic ecosystem is quite different from that of the Crustaceans, the usual particle-feeders of the pelagos: thus, turn-over time of Salps is much shorter and their predators are different, which means the terminal production may be changed after a Salps bloom.

The present paper is restricted to the growth rates of *T. democratica* in the atoll of Tikehau, as assessed by two different and independent methods, since this parameter is not well documented yet. The first data on this species were presented by HERON (1972) for offshore waters of the tropical Pacific and Indian Oceans. At the time, doubling times of 0.7-1.7 days were found surprisingly short. Later, DEIBEL (1982) reported longer doubling times on animals breeded in the laboratory, and caught off Florida and Georgia (USA): 1.5 to 33 days, depending on the development stage. Data, similar to HERON's were found on another Salp, *Salpa fusiformis*, in the Gulf of Guinea by LE BORGNE (1983), its average turn-over time being 0.7 day during a bloom. Finally, in a recent study on *T. democratica*, HERON and BENHAM (1985) present hourly length increments of 20 %, which is roughly equivalent to a doubling time of 0.2 day (5 hours), provided the length variation is taken as a linear function of time at this stage. As far as we know, the values cited above are the only ones for Salps and we found it useful to report on other ones dealing with a rather rich and warm (30 ºC) environment, those two characteristics being known to influence the growth rates.

METHODS

Two different methods have been used to assess the growth rate. That of HERON and BENHAM (1985) is based on counts and identifications of developmental stages, whereas the second method uses measurements of the elemental chemical composition and metabolic rates (C:N:P ratios method; LE BORGNE, 1978).

1. Assessment of growth rates from the number of buds per chain and the offspring to parent ratio (method of HERON and BENHAM, 1985)

Among Salps, asexually reproducing solitary forms (*i.e.* oozooids) alternate with aggregated forms (*i.e.* blastozoids) with a sexual reproduction. Recently, HERON and BENHAM (1985) established that the growth rate, G, was related to the number of buds produced by each chain of the oozooid, on the one hand, and the ratio between the number of blastozoids and that of oozooids, on the other hand:

G = 0.576 — 0.0876 Ln (buds per chain) — 0.0211 Ln (blasto/oozoo)   (1)

The growth rate, G, is expressed as a percentage of the length per hour and, according to the authors, would be known with a precision of 0.67 to 0.78 % of the increment, which is quite satisfactory.

It is worth pointing out that the assessment of G is based on identifications and does not depend on the duration of the preservation of the individuals. However, it is dependent on the sampling, which is meant to be representative of the various development stages in the actual environment. In the atoll, sampling was performed with a WP-2 net (Anonyme, 1968), of ¼ square meter at the mouth and a mesh-size of 200 μm, towed vertically from the bottom to the surface, that is roughly equivalent to a 5 m³ filtered volume (see LE BORGNE *et al.*, 1986, Annexe 2). Since Thaliaceans concentrations were high (Table II), and their avoidance capability and size were small, we can assume the sampling was satisfactory, although there is too low a number of samples (3 hauls) to prove it statistically.

At last, it is worth noting that the growth rate, G, is concerned with the length of the individuals, but not with their weight, since HERON and BENHAM (1985) do not provide any equivalence between the two variates.

2. Assessment of the production rate by the C:N:P ratio method (LE BORGNE, 1978)

The production rate which can be calculated by this method is concerned with gross production, *i.e.* before losses from moulting (when Crustaceans are concerned) or release of eggs and larvae, occur. The calculation is based on measurements of excretion or respirations rates on the one hand, and on values of the net growth efficiency, K_2, which can be assessed from C:N (carbon: nitrogen) or N:P (nitrogen: phosphorus) ratios of preys, metabolic losses, constituents and assimilation efficiencies of predators, on the other hand. As far as *T. democratica* is concerned, preys can be taken as organic particles from 0.7 to 35 μm because they are the most abundant and they can be used by Salps (HARBISON and GILMER, 1976). Table I sums the different steps of the calculation up, for the N:P ratio, the details being presented in CORNER and DAVIES (1971) or LE BORGNE (1978).

Excretion or production rates are amounts of carbon, nitrogen or phosporus excreted or produced by one milligram of dry weight and one hour. When production to biomass (P:B) ratios need to be calculated, the same weight unit must be used, so that measurements of the chemical composition of *T. democratica* are required. These are referred to as % C, N, P on Table I, and are percentages of carbon, nitrogen or phosphorus in the dry weight. Turn-over is the time necessary for the biomass to double

TABLE I

Parameters used for the assessment of production rates by the C/N/P ratios method

Éléments entrant dans le calcul de la production par la méthode des rapports C N P

```
a₁ = particulate N:P (atoms)          K₂,ₚ = (a₁.a₄-a₂).(a₃-a₂)⁻¹   (2)
a₂ = N excretion : P excretion        K₂,ₙ = a₃ K₂,ₚ . (a₁.a₄)⁻¹   (3)
a₃ = constituent N:P                  Pₙ,ₚ = K₂. Tₙ,ₚ . (1-K₂)⁻¹   (4)
a₄ = N assimilation efficiency (DN):DP Pc = Pₙ . a₃
Tₙ,ₚ = total N or P excretion rate     P:B = Pc,ₙ,ₚ .(10x%C,N,P)
Pc,ₙ,ₚ = C,N,P production rate
%C,N,P = percentage of C,N,P in the d.w.
```

(without any mortality) and, therefore, is the inverse of the P:B ratio.

Individuals, the production of which was assessed by this method, were caught in the same way as those of the other method. They were incubated for 6.5 to 10.0 hours at 29.5 °C in 1 l flasks filled with non filtered sea water (LE BORGNE *et al.*, 1986, Annexe 5) for subsequent measurements of total nitrogen and phosphorus excretions. The latter includes inorganic forms as measured with the U.V. irradiation method of ARMSTRONG and TIBBITTS (1968). There were 12 excretion measurements between the 6th and the 10th of April; atomic a₃ ratio and % C, N, P of Table I were measured on the 9th and 10th (see Annexe 3, LE BORGNE *et al.*, 1986) on sorted animals that were subsequently grinded and poored into "CHN" boats for elemental composition analysis. Similarly, a₁ atomic ratio for particulate matter, is calculated on results of the 9th and 10th of April (LE BORGNE *et al.*, 1986). Finally, no direct measurement of assimilation efficiencies in terms of nitrogen and phosphorus were made, so that a₄ was taken as equal to one, following the discussion of LE BORGNE (1982).

RESULTS

1. Growth rates obtained with the method of HERON and BENHAM (1985)

The number of buds per chain is the number "produced by each solitary parent and is determined by the number of buds in its chain and the number of chains per parent, which is usually three. The average number of chains is determined by the proportion of younger reproducing adults, which so far have had only one or two chains (stages I and J), to the older adults, which so far have had three (stages K-M)" (HERON and BENHAM, *id.*). Applying the latter definition to values of the 30th of March (Table II) would lead to an average number of chains greater than three, which is wrong: 3.24 (133:41). Therefore the average number of chains per adult is more likely the ratio between the number of chains

(one for each stage I, two for J, three for K-M) and the total number of individuals of stages I to M. Using values of Table II for the three samples, we then get mean numbers of chains of 2.04 (355:174) on the 30th of March, 2.18 (310:142) on the 5th of April and 2.17 (163:75) on the 9th of April.

The mean number of buds per solitary parent (oozooid) is got by dividing the total number of buds by the observed number of individuals. Using values on Table II leads to the following number of buds: 39.73 (5204:131), 42.47 (4332:102) and 28.35 (1134: 40) for the three dates cited before, respectively.

Finally, the average number of buds per chain is the ratio between the mean number of buds per oozooid, which we have just been considering, and the mean number of chains, that is 17.74 (39.73:2.04), 18.47 (42.47:2.30) and 11.57 (28.35:2.45), respectively.

The second parameter used in the calculation of G (equation (1)), is the ratio between the number of the blastozoids from stages B to E, and the number of oozooids of stages I to M. It is equal to 31.67, 12.21 and 39.08 for the three samples.

Using the two sets of parameters in equation (1), leads to the following three hourly growth rates, expressed as proportions of the length:

```
Sample of the 30/3 : G = 0.251
Sample of the 5/4 : G = 0.268
Sample of the 9/4 : G = 0.284
```

Such values mean that length of *T. democratica* increases by 25 to 28 % per hour, which is very quick for the Animal Realm. The second method makes it possible to confirm (or infirm) such high values.

2. Assessment of the hourly weight increment by the C:N:P ratios method

Values of hourly production rates referring to carbon, nitrogen and phosphorus (Pc, Pₙ, Pₚ) and the P:B ratios are presented on Table III. They appear to be very high, since the hourly weight increase is 33 to 36 %, according to the element which is considered. Actually, these values should be equal, other-

Numbers of individuals of each developmental stage of the solitary generation (oozooids). The first line of each stage refers to the sample of 30.3.85, the second to that of the 5.4 and the third to the 9.4.85

Nombre d'individus des différents stades de développement d'oozoïdes de Thalia democratica, comptés sur trois échantillons : 30.3.85 sur la première ligne de chaque stade, 5.4 sur la seconde et 9.4 sur la troisième

Stage	Short description of the stage (after HERON and BENHAM)	Total number of individuals	Total number of buds
F	embryo released from its parent, with a large aeloblast and placenta attached	42 24 38	
G	young stage with a reduced aeloblast and placenta	29 24 28	
H	young stage with no segmentation in its stolon	112 32 66	
I	young stage with stolon segmented	34 16 22	
J	mature stage with two chains segmented	99 84 18	3548 3684 444
K	mature chain with three chains segmented	32 18 22	1656 648 690
L	mature stage with at least one chain released	0 8 5	
M	senile stage with all chains released	9 16 8	

wise the body constitution would be modified on a short-term basis. Such slight differences originate from rounding errors in the calculations.

DISCUSSION

Four problems may be discussed about the results on growth rates which have just been presented. First, can the observed results originate from methodological errors? Secondly, do the two methods give comparable results, since one produces length increments and the other one, raw weight increments, before any loss or predation takes place in the environment? Thirdly, what is the reason for such

quick growth rates? Finally, consequences of high growth rates of *T. democratica* on the pelagos will be dealt with, briefly.

1. The influence of the methodology

Although both methods give very high rates, their use may be questioned in the present case. Thus, HERON and BENHAM's (1985) figures clearly show that their relationships have been established for a minimum number of buds per chain of 30, whereas all our value lie below 20. We wondered whether our calculation of this parameter was correct, since their definition of the number of chains did not look

TABLE III

Mean values of Table I parameters applied to *Thalia democratica* and used for the calculation of the net growth efficiency, K_2, the hourly production rate P and the P:B ratio for carbon, nitrogen and phosphorus

Valeurs moyennes des paramètres du tableau I pour Thalia democratica, *nécessaires au calcul du rendement net en croissance, K_2, du taux de production horaire, P et du rapport P:B, pour le carbone, l'azote et le phosphore*

Parameter	Number of replicates	Mean	Results
a_1	25	13.9	$K_{2,P}$ = 0.519
a_2	12	6.9	$K_{2,N}$ = 0.761
a_3	2	20.4	P_N = 2.2467/mg dw./h
%C	2	1.91	P_P = 0.2458 "
%N	2	0.67	P_C = 6.8125 "
%P	2	0.0725	$P:B_N$ = 33.5%
T_N	12	0.0504	$P:B_P$ = 33.9%
T_P	12	0.0073	$P:B_C$ = 35.7%

precise to us, as mentioned in the "Results". So we tried two other ratios: (1) the number of individuals of stages I and J to the number of individuals of stages K to M, following the formulation of HERON and BENHAM; (2) the number of chains of stages I to M to the total number of individuals, taking two chains per individual for stage I instead of one in our own calculation (see "Results"). With (1), the mean number of chains would be 3.24, 2.38 and 2.17 for the three samples of Table II, respectively. With (2), the values are 2.24, 2.30 and 2.45, respectively. Using the same number of buds per solitary as previously (see "Results"), would lead to values for the mean number of buds per chain of 12.26, 17.84 and 24.67 with (1) and 19.48, 19.48 and 13.06 with (2). These are slightly different than those presented before (17.74, 18.47 and 11.57), but still less than 30 and leading to very close results for the growth rates, G: 0.284, 0.271 and 0.218 with (1) and 0.243, 0.263 and 0.274 with (2). Therefore, we may admit that the values of G are quite the same whatever the way of calculating the mean number of chains. It would, of course, be worth testing the relationship of HERON and BENHAM for the data range of the number of chains found in Tikehau. On the other hand, the second parameter assessed in eqn (1), *i.e.* the ratio between the number of blastozoids and that of the

oozooids, does lie in the range presented by HERON and BENHAM (1985).

The second set of possible methodological bias deals with the C:N:P ratios method:

— When important secretions of Thaliaceans are measured together with excretion, production rates assessed by this method are overestimated (formula (4), Table I). However, high percentages of excreted ammonium or phosphate (LE BORGNE *et al.*, 1986; Annexe 5) would prove that secretions of organic compounds, if they occurred, were negligible.
— P:B ratio may be wrong if percentages of C,N,P in the dry weight are erroneous. When these are low, P:B increases for a given production rate referring to the dry weight. Such percentages are low indeed when compared to the values of the literature (Table IV), so that an overestimation of P:B cannot be impossible. A reason for low percentages could be the "salt effect", *i.e.* an increase of the dry weight without any for C, N, or P.

2. Comparison of the growth rates produced by the two methods

Hourly growth rates derived from C:N:P ratio method cannot readily be compared with those based on life history parameters of the Salps. First, they must be assumed to be representative average values, thus neglecting diel variations of the N:P ratios or excretion rates. Such variations have been shown in other regions of the world ocean and may also take place in the atoll of Tikehau. However, working conditions did not make it possible to study this kind of short-term variations.

But, the main problem deals with the conversion of length data produced by HERON and BENHAM's (1985) method, into weight data. These authors have developped a new weight-length relationship for *T. democratica*, "using a method which overcomes the bound water problem of gelatinous organisms" (HERON and BENHAM, 1984), but unfortunately we have not been able, so far, to know more about it. Therefore, results presented by DEIBEL (1982) on the same species, caught off North American coasts, in a similar water temperature as HERON and BENHAM's (1985), *i.e.* 20 °C, will be used. This relationship between weight (W) and length (L) is: W = 0.8 $L^{2.1}$ (5). Now, we are looking for the relationship between G and $\Delta W/W.\Delta t$, using eqn (1), which gives G as a function of $\Delta L/L.\Delta t$ and (5):

$$\left. \begin{array}{l} G = \dfrac{\Delta L}{L} \times \dfrac{1}{\Delta t} \\[2mm] W = 0.8 \times L^{2.1} \end{array} \right\} \Rightarrow \begin{array}{l} \dfrac{\Delta L}{\Delta t} = G \times L \Longleftrightarrow \dfrac{\Delta L}{\Delta W} \times \dfrac{\Delta W}{\Delta t} = G \times L \\[2mm] \dfrac{\Delta W}{\Delta t} = G \times L \times \dfrac{\Delta W}{\Delta L} = G \times L \times 0.8 \times 2.1 \times L^{1.1} \end{array}$$

$$\dfrac{\Delta W}{\Delta t} = G \times 2.1 \times W \Longleftrightarrow G' = \dfrac{\Delta W}{W} \cdot \dfrac{1}{\Delta t} = 2.1 \times G$$

TABLE IV

Percentages of the dry weight in C, N, P and atomic constituent ratios for Thaliaceans in the literature and the present study

Valeurs comparées des teneurs du poids sec des Thaliacés en C, N et P et de leurs rapports atomiques, dans la littérature et à Tikehau

Reference	Species	%C	%N	%P	C:N	N:P
CURL (1962)	Tuniciers	7-10	0.3-1.5	0.14	2.7-7.7	23-47
MADIN et al. (1981)	Salpes	1.07	-	-	-	-
IKEDA et MITCHELL (1982)	Salpes	4.7-10.1	1.2-2.8	0.09-0.16	-	30-39
LE BORGNE (1982)	Salpa fusiformis	9.2	2.1	0.0195	4.6	23.9
LE BORGNE et ROGER (1983)	Salpes	8.6	2.2	0.20	4.65	24.2
Présent article :	Thalia democratica	1.91	0.67	0.0725	3.33	20.4

In other words, the weight increment is 2.1 times the length increment during Δt. For $G = 0.251$ on the 30th of March, 0.268 on the 5th of April and 0.284 on the 9th, we get $G' = 0.527, 0.563$ and 0.596, respectively. In one hour, the weight would be increased by 53 to 60 % according to the sample considered. Such values match quite well with those of the other method (Table III), bearing in mind that the conversion from length into weight is approximate and that measurements used for the C:N:P ratios method were made at the end of the study, whereas life-history parameters were determined at the beginning, the middle and the end of the study.

3. The reasons for high growth rates

Explanations for the high growth rates that were found for *T. democratica*, deal with the environmental factors and the caracteristics of the populations. It is quite true that growth rates measured or computed on natural populations, with a great proportion of young stages, are higher than growth rates of an individual during its life cycle and, *a fortiori*, larger than the inverse of the generation time which is used sometimes (LE BORGNE, 1982). The rather high concentrations of organic particles in the lagoon is a second reason for the observed growth rates. This trophic factor was found to be the main factor of variation of growth of *T. democratica* by HERON and BENHAM (1984), the thermal effect being less important. However, the latter probably explains the difference in turn overs found by HERON and BENHAM (1984) and LE BORGNE (1983) at temperatures ranging between 16.5 and 22 °C and those of the lagoon of Tikehau atoll at 30 °C. Thus, for a non-limiting amount of food, metabolic rates of poikilothermic animals are known to increase with temperature. LE BORGNE *et al.* (1986) report that zooplankton ingestion, including the Salps, stands for 58 % of the ^{14}C uptake by phytoplankton, a result showing that the amount of preys was not limiting the Salps growth.

4. Consequences of high growth rates on the environment

When the weight of Thaliaceans can be increased by 33 to 60 % per hour, according to the method used and the period, swarms occur rapidly. But, as just mentioned, the amount of particles was not found limiting, unless they were of low energetical value, so that Salps probably had not reached their maximum at the end of the present study. They were not limited by predation, either, because the usual Hyperiid Amphipods (LAVAL, 1980) were not observed in their body. At last, competition with other filter-feeders is unlikely, because Thaliaceans are among the most efficient of the pelagic environment. So, it is quite reasonable to think that this Salps swarm was clearing the particles of the lagoon, after or during a "bloom" of phytoplankton or particles produced by the reef. Their origin is not clear, although BLANCHOT and MOLL (1986) report great amounts of setae of the Diatom *Chaetoceros sp.* in the 35-200 μm size-fraction, thus indicating a former Diatom bloom. Further observations, made in July 1985, did not show any more Salps in the lagoon, proving the temporary feature of this kind of phenomenon. Unfortunately, their effect on the terminal production is not well documented (LE BORGNE, 1983).

CONCLUSION

Growth rates of *Thalia democratica*, as got by two different methods, are the quickest ever reported for Thaliaceans and Metazoa, probably. Thus, the weight would be increased by 33 to 60 % per hour. However, such values should be taken with care, because they are based on a few measurements only, and out of the limits of the methods, sometimes. An interesting test would consist in making direct weight measurements during a swarm at 30 °C and compare the data with those of the present paper. However, Salps proliferations are still unpredictable and one has just got to be there when they occur.

REFERENCES

Anonyme, 1968. — Zooplankton sampling. *Monographs Oceanogr. Methodol.*, 2, UNESCO, Paris, 174 p.

ARMSTRONG (F. A.) and TIBBITTS (S.), 1968. — Photochemical combustion of organic matter in seawater for nitrogen, phosphorus and carbon determination. *J. Mar. Biol. Assoc. U.K.*, 48 : 143-152.

BLANCHOT (J.) et MOLL (P.), 1986. — Contribution à l'étude de l'atoll de Tikehau. Le zooplancton. Composition faunistique de la fraction 35->2000 μm. *ORSTOM Tahiti, Notes et Documents Océanogr.*, 28 : 169-180.

CORNER (E. D. S.) and DAVIES (A. G.), 1971. — Plankton as a factor in the nitrogen and phosphorus cycles in the sea. *Adv. Mar. Biol.*, 9 : 101-204.

CURL (H.), 1962. — Standing crops of carbon, nitrogen and phosphorus and transfer between trophic levels in Continental Shelf waters South of New York. *Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer.*, 153 : 99-107.

DEIBEL (D.), 1982. — Laboratory determined mortality, fecundity and growth rates of *Thalia democratica* Forskal and *Dolioletta gegenbauri* Uljanin (Tunicata, Thaliacea). *J. plankton Res.*, 4 (1) : 143-153.

HARBISON (G. R.) and GILMER (R. W.), 1976. — The feeding rates of the pelagic tunicate *Pegea confederata* and two other salps. *Limnol. Oceanogr.*, 21 (4) : 517-528.

HERON (A. C.), 1972. — Population ecology of a colonizing species, the pelagic Tunicate *Thalia democratica*. I. Individual growth rate and generation time. *Oecologia*, 10 : 269-293.

HERON (A. C.) and BENHAM (E. E.), 1984. — Individual growth rates of salps in three populations. *J. plankton Res.*, 6 (5) : 811-828.

HERON (A. C.) and BENHAM (E. E.), 1985. — Life history parameters as indicators of growth rate in three salp populations. *J. plankton Res.*, 7 (5) : 365-379.

IKEDA (T.) and MITCHELL (A. W.), 1982. — Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic zooplankton in relation to their body size and chemical composition. *Mar. Biol.*, 71 : 283-298.

LAVAL (P.), 1980. — Hyperiid Amphipods as Crustacean parasitoids associated with gelatinous zooplankton. *Oceanogr. Mar. Biol. Rev.*, 18 : 11-51.

LE BORGNE (R.), 1978. — Évaluation de la production secondaire planctonique en milieu océanique par la méthode des rapports C/N/P. *Oceanol. Acta*, 1 : 107-118.

LE BORGNE (R.), 1982. — Zooplankton production in the eastern tropical Atlantic Ocean : net growth efficiency and P:B in terms of carbon, nitrogen and phosphorus. *Limnol. Oceanogr.*, 27 : 681-698.

LE BORGNE (R.), 1983. — Note sur les Proliférations de Thaliacés dans le golfe de Guinée. *Océanogr. trop.*, 18 (1) : 49-54.

LE BORGNE (R.) et ROGER (C.), 1983. — Caractéristiques de la composition et de la physiologie des peuplements hauturiers de zooplancton et micronecton du Golfe de Guinée. *Océanogr. Trop.*, 18 (2) : 381-418.

LE BORGNE (R.), BONNET (S.) et CHARPY (L.), 1986. — Contribution à l'étude de l'atoll de Tikehau. Le zooplancton. Biomasse, composition élémentaire, respiration, excrétion et production. *ORSTOM Tahiti, Notes et Documents Océanogr.*, 28 : 115-152.

MADIN (L. P.), CETTA (C. M.) and Mc ALISTER (V. L.), 1981. — Elemental and biochemical composition of Salps (Tunicata, Thaliacea). *Mar. Biol.*, 63 : 217-226.