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Food ingestion and assimilation by *Hyale media* (Dana, 1853) (Crustacea - Amphipoda)

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- *Abstract:* The feeding of *Hyale media* was analysed under laboratory conditions in winter and summer temperatures. The results showed that assimilation rates increased following food ingestion rates and decreased when egestion rates increased. In winter temperatures no significant differences were found in the assimilation rates among developmental stages and sexes. In summer temperatures assimilation rates for ovigerous and non-ovigerous females were higher than those found for adult and young males. Although not statistically analysed, mean assimilation efficiencies were highest among ovigerous females and adult males, in summer. The quantitative and qualitative variations found in the assimilation efficiency and rates were explained by the differential effect of temperature on the specific growth rate and in the physiological conditions of each growth stage concerned.

- *Descriptors: Hyale media*, Feeding experiments, Ingestion, Developmental stages, Assimilation, Organic carbon.

- *Descritores: Hyale media*, Experimentos de alimentação, Ingestão, Estádios de desenvolvimento, Assimilação, Carbono orgânico.

Introduction

Recent studies on the feeding biology of gammaridean species other than *Hyale media* have been undertaken by Nicotri (1977; 1980), Vassalo & Steele (1980), Shacklook & Croft (1981), Brawley & Adey (1981), Price & Hylleberg (1982), Shacklook & Doyle (1983) and Willoughby (1983). Assimilation efficiency in the group, using gravimetric and/or radioisotope methods, was investigated by Tsikhon- Lukanina *et al.* (1968), Hargrave (1970; 1972), Kititsina (1975), Brenner *et al.* (1976), Zimmerman *et al.* (1979), Pomeroy & Levings (1980) and Nielsen & Kofoed (1982). The present account is concerned with laboratory studies undertaken to analyse the quantitative aspects of the feeding of *H. media*, using the gravimetric method, allied to the carbon content of the food items. This species was chosen because it occurs abundantly on the phytal of rocky shores of São Paulo State and it is also an important food source for local fish (Tararam & Wakabara, 1981, 1982; Wakabara *et al.*, 1983; Tararam *et al.* 1986).

Material and methods

Specimens of *H. media* were obtained at Praia do Poço in the southern coast of the São Paulo State, Brazil (24°12'S and 46°47'W). The species is a common local inhabitant, found throughout the year (Wakabara *et al.*, 1983). The food items utilized in the ingestion experiments were the seaweeds *Sargassum stenophyllum* Martius, *Ulva fasciata* Delile, *Padina vickersiae* Hoyt and animal food, comprising the gammarids *Cymadusa filosa* Savigny, 1816, *Ericthonius brasiliensis* (Dana, 1853) and *Hyale media* (Dana, 1853). These food items are found in the sampling sites throughout the year in sufficient quantities to be potentially utilized as food.

In the laboratory, the specimens of *H. media* were maintained in an aquarium (28 l capacity) containing aerated seawater from the collection site. The separation

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of the developmental stages and sexes was based on the study of the *H. media* life cycle by Leite (1976).

For the experiments animals were separated into two groups:

1) usually immature males and females (♂$_1$, ♀$_1$) with nine or 10 articles in antenna 1, comprising developmental stages IV and V;

2) mature males with large gnathopods (♂$_2$), mature and ovigerous females (♀$_2$), both with 11 or 12 articles in antenna 1, comprising developmental stages VI and VII.

The specimens were acclimatized for 48 hours, at the experimental temperatures, 21.1 ± 0.8°C and 26.8 ± 0.6°C, and salinity, 34.18 ± 0.80 ‰. Experimental temperatures were approximately equal to the mean temperature found in the sampling site, during winter and summer, respectively. After a starvation period of 12 hours, three individuals of the same sex and group were placed into beakers (500 ml), each one containing only one type of food. A chance of choice of food was not given to *Hyale*. Therefore, the term "preference" used elsewhere in the present work, means a "higher assimilation of a food item relatively to the others". Animal and plant food average weight were 1.0 ± 0.5 mg (n = 66) and 5.0 ± 3.0 mg (n = 192), respectively. The number of experiments for each group and sex, and for each type of food ranged from 7 to 9. The range of dry weight of the animals and the corresponding mean values are shown in Table 1. The feeding period, in the dark and constant aeration, was 22 hours. Each set of experiments had one beaker as control, containing seawater from the collection site with food and without *H. media*.

Table 1. Mean values and range of *Hyale media* dry weight (mg)

Sex/Group	Winter	($\bar{x}$)	(n)	Summer	($\bar{x}$)	(n)
♂$_2$	2.0-4.0	2.8	33	2.2-4.6	3.3	33
♀$_2$	0.9-2.0	1.4	34	0.9-2.5	1.7	34
♂$_1$	1.2-2.6	1.7	33	0.7-2.6	1.6	29
♀$_1$	0.7-2.0	1.1	33	0.7-1.6	1.1	30

After the feeding period, individuals remained without food for 36 hours to eliminate the non-assimilated food. A silk net placed over the bottom of the beakers prevented the faeces from being ingested. The faecal pellets expelled were collected with the aid of a dissecting microscope and pipette, and placed over Whatman GF/C filter pre-combusted at 600°C. The filters containing the faecal pellets were kept in a dessicater for 24 hours and then frozen at - 10°C for further analyses. This procedure should minimize bacteria proliferation which, on account of their high growth rates, might introduce large errors into the carbon content of the organic matter, and hence, into the food assimilation rates and efficiency (Conover, 1966; Johannes & Satomi, 1966; Frankenberg *et al.*, 1967; Lawton, 1970). After the feeding experiments the individuals were dried for 24 hours at 90°C, and then weighed.

The quantity of carbon in the food items and faeces necessary to estimate the amount of ingested, egested and assimilated carbon was analytically determined according to the methodology of El Wakeel & Riley (1957), modified by Marshall & Orr (1964) and Strickland & Parsons (1968).

Carbon content of parts (in weight) of a same food item showed variation. The aliquot of food given to *Hyale* was estimated by weight and, as it would be eaten, could not have its carbon content determined. In order to have a more precise value of its carbon content, the relationship between the weight of the food item utilized by *Hyale* and, an average value of carbon of every food item obtained previously, was analyzed.

Pieces of algae and animals were weighed on an analytical balance to the nearest 0.1 mg and the average organic carbon content of each food item was determined. The results were expressed as mg C/mg of food. The quantity of ingested carbon was estimated, by the difference between the initial and final weights of the food given. The amount of carbon in the faeces was determined after the feeding period was over by dichromate titration of the faecal material collected in fiber-glass filters. In this paper assimilation is defined as the difference between ingested and egested carbon (faeces). Results were expressed as g of carbon . mg of dry weight of *H. media*$^{-1}$. hour^{-1}.

The assimilation efficiency, defined as the percentage of ingested material absorbed during the passage of food through the gut (Hargrave, 1970), was obtained by:

$$Ca = \frac{A - C}{A} . 100$$

where Ca is the percentage of assimilated organic carbon, C is the quantity of organic carbon in the faeces and A is the quantity of organic carbon ingested with food. Data given in Figures 1-3 represent the results of each experiment using three individuals. The percentage of assimilation for each stage and each type of food was based on the average of 7-9 experiments. The data were analysed through a multi-way analysis of variance model. For the pair-wise comparison Tukei's method was used (Winer, 1971). A 5% significance level was used for all comparisons.

Results and discussion

The carbon content of the food items used in the present experiments seems to vary among different types of organisms (plant or animal). However, data obtained are insufficient to infer carbon content variation in food and/or throughout the year. Apparently, *Sargassum* is the organism with the highest carbon content (Table 2).

The assimilation efficiency data (Table 3) are lower when compared with data from literature on the same food items. Tsikhon-Lukanina *et al.* (1968) reported that the amphipod *Pontogammarus maeoticus* fed on dried *Cladophora*, showed a mean value of 65 ± 4.1% assimilation. *Eogammarus confervicolus* (another

Table 2. Mean carbon content of the food items utilized in *Hyale media* experiments (mg carbon/mg food)

Month/Year	*Sargassum*	*Ulva*	*Padina*	Animal food
09/78	0.2256	-	-	-
09/78	0.1899	-	-	0.1782
10/78	0.2687	-	-	0.2173
11/78	0.1728	0.1745	-	0.1903
12/78	-	-	0.1659	-
03/79	0.1860	0.1509	0.1604	0.1587
06/79	-	0.1468	0.1408	-
07/79	0.1887	-	-	-
08/79	-	-	-	0.2044

gammaridea) fed on *Ulva lactuca* assimilated 62% of this alga (Pomeroy & Levings, 1980).

A highly significant correlation is found between the weight of the ingested food and the carbon content of an equal weight of the same food item (Fig. 1) suggesting that the use of the carbon parameter is adequate to analyze *H. media* feeding. On account of this, the words ingestion, egestion and assimilation to be used in this paper refer to the carbon content and not to the weight of the food.

Using the present methodology, and considering each season separately, assimilation rates depend upon the ingestion and egestion rates, in such a way that assimilation rates increase following ingestion rates (Figs 2a, b) and should decrease as food egestion rates increase (Figs 3a, b). The latter consideration is not so clearly inferred from the present experiments because of the large data dispersion. Egestion rates showed a minimum value for *Sargassum* in winter when its assimilation rate was highest. In summer, *Ulva* and animal food were the least egested items, and usually with highest assimilation rates (Table 4).

The general conclusion that assimilation rates increase following ingestion holds when the variation from winter to summer is considered. Carbon ingestion rates were not significantly different from winter to summer, except one food item, *Ulva*, which showed higher ingestion rate in summer. Egestion rate of *Ulva* did not change significantly from winter to summer. Therefore, the rate of *Ulva* assimilation is higher in summer.

In two seasons, the variation of the mean ingestion, egestion and assimilation rates and of the efficiency of assimilation at every growth (stages 1 and 2) and reproductive stages (♂ and ♀) considered, may be accounted for by the differences in the average weight and also in the physiological characteristics of the growth and reproductive stages. In winter, males (♂$_1$ and ♂$_2$) seem to show higher mean assimilation efficiency than females (♀$_1$ and ♀$_2$). Males were larger than females (ANOVA, $p \leq 0.05$). In summer, males which have the largest average weight showed the highest mean assimilation efficiency. Therefore, assimilation efficiency seems to be higher in the largest animals on account of their biomass and so, on account of the increment in the maintenance cost due to the weight increase. However, the difference in the mean weight between ♀$_2$ and ♂$_1$ in summer, is too small to account for the difference found in the assimilation efficiency. On the other hand, the difference between ♀$_2$ and ♂$_2$ mean weights, in summer, is too large to account for the small difference found in the assimilation efficiency (Table 3).

Assimilation rates did not show the same pattern found for assimilation efficiency. No significant differences were found in winter among sex and developmental stages concerning assimilation rates. In summer, assimilation rates of ovigerous and non-ovigerous females were significantly higher than for males (ANOVA, $p \leq 0.05$). As assimilation rates do not depend on the weight of the animal (μgC/mg dry weight/h), they reflect better the influence of physiological conditions on food assimilation by *Hyale*.

The quantitative and qualitative variation, from winter to summer, in the assimilation efficiency and rates, may be explained by the differential effects of temperature on the specific growth rate, as well as on the physiological conditions of each growth stage concerned (Kinne 1960, 1961; Steele & Steele, 1973; Kock-Kallnback & Meijering, 1977; Nilsson 1974, 1977; Welton & Clarke, 1980).

A change in temperature determines quantitative alterations in the growth characteristics of individuals which are probably compensated by a qualitative change

Table 3. Values of assimilation efficiency and assimilation rates by *Hyale media*

Sex/group	Food item	Number of experiments	Mean dry weight of *H. media* (mg)	Assimilation efficiency (%)	Mean assimilation rates (µg/mg dry weight/h)
			WINTER		
♂$_2$	Animal food	9	2.80	58	1.3
	Sargassum	8	3.20	73	1.8
	Ulva	8	2.60	47	1.1
	Padina	8	2.70	60	1.2
	Mean of all experiments		2.83	60	1.3
♀$_2$	Animal food	9	1.30	49	1.8
	Sargassum	8	1.60	67	3.1
	Ulva	9	1.40	44	1.5
	Padina	8	1.50	38	1.4
	Mean of all experiments		1.45	50	1.9
♂$_1$	Animal food	9	1.70	66	2.0
	Sargassum	8	2.10	66	2.2
	Ulva	8	1.50	39	1.7
	Padina	8	1.60	48	2.0
	Mean of all experiments		1.72	55	1.9
♀$_1$	Animal food	8	1.00	52	2.1
	Sargassum	8	1.20	63	2.3
	Ulva	9	1.00	26	1.2
	Padina	8	1.00	28	1.5
	Mean of all experiments		1.05	42	1.7
			SUMMER		
♂$_2$	Animal food	8	3.10	74	2.1
	Sargassum	8	3.40	65	2.8
	Ulva	9	3.40	73	2.3
	Padina	8	3.20	55	1.6
	Mean of all experiments		3.30	67	2.2
♀$_2$	Animal food	9	1.40	84	4.5
	Sargassum	8	1.80	44	1.8
	Ulva	8	1.80	75	5.6
	Padina	9	1.70	47	1.8
	Mean of all experiments		1.67	63	3.4
♂$_1$	Animal food	8	1.50	65	1.9
	Sargassum	8	1.70	45	1.7
	Ulva	6	1.20	58	3.7
	Padina	8	2.00	51	2.5
	Mean of all experiments		1.60	55	2.4
♀$_1$	Animal food	8	1.10	60	3.0
	Sargassum	8	0.90	60	5.9
	Ulva	7	1.20	65	5.1
	Padina	7	1.10	39	2.3
	Mean of all experiments		1.07	56	4.0

Table 4. Mean values of carbon ingestion, egestion and assimilation by *Hyale media*

Sex/group	Food item	Number of experiments	Mean dry weight of *H. media* (mg)	Mean carbon ingestion (µg/h)	Mean carbon egestion (µg/h)	Mean carbon assimilation (µg/h)
			WINTER			
♂$_2$	Animal food	9	2.80	6.31	2,64	3.67
	Sargassum	8	3.20	7.15	1.93	5.22
	Ulva	8	2.60	6.07	3.24	2.83
	Padina	8	2.70	5.63	2.28	3.35
	Mean of all experiments		2.83	6.29	2.52	3.77
♀$_2$	Animal food	9	1.30	5.21	2.67	2.54
	Sargassum	8	1.60	7.53	2.48	5.05
	Ulva	9	1.40	5.27	2.94	2.33
	Padina	8	1.50	5.70	3.54	2.16
	Mean of all experiments		1.45	5.92	2.90	3.02
♂$_1$	Animal food	9	1.70	5.17	1.76	3.41
	Sargassum	8	2.10	7.37	2.49	4.88
	Ulva	8	1.50	7.04	4.30	2.74
	Padina	8	1.60	6.59	3.44	3.15
	Mean of all experiments		1.72	6.54	2.99	3.55
♀$_1$	Animal food	8	1.00	4.00	1.94	2.06
	Sargassum	8	1.20	4.64	1.72	2.92
	Ulva	9	1.00	4.83	3.57	1.26
	Padina	8	1.00	5.82	4.18	1.64
	Mean of all experiments		1.05	4.82	2.85	1.97
			SUMMER			
♂$_2$	Animal food	8	3.10	7.78	2.01	5.77
	Sargassum	8	3.40	11.75	4.12	7.63
	Ulva	9	3.40	11.04	3.00	8.04
	Padina	8	3.20	7.78	3.52	4.26
	Mean of all experiments		3.30	9.58	3.16	6.42
♀$_2$	Animal food	9	1.40	7.24	1.15	6.09
	Sargassum	8	1.80	7.77	4.34	3.43
	Ulva	8	1.80	12.00	2.98	9.02
	Padina	9	1.70	6.14	3.25	2.89
	Mean of all experiments		1.67	8.28	2.93	5.35
♂$_1$	Animal food	8	1.50	7.51	2.59	4.30
	Sargassum	8	1.70	7.28	3.97	3.31
	Ulva	6	1.20	7.01	2.93	4.08
	Padina	8	2.00	9.18	4.50	4.68
	Mean of all experiments		1.60	7.74	3.49	4.10
♀$_1$	Animal food	8	1.10	6.03	2.42	3.61
	Sargassum	8	0.90	9.04	3.62	5.42
	Ulva	7	1.20	8.61	3.02	5.59
	Padina	7	1.10	6.95	4.22	2.73
	Mean of all experiments		1.07	7.65	3.32	4.33

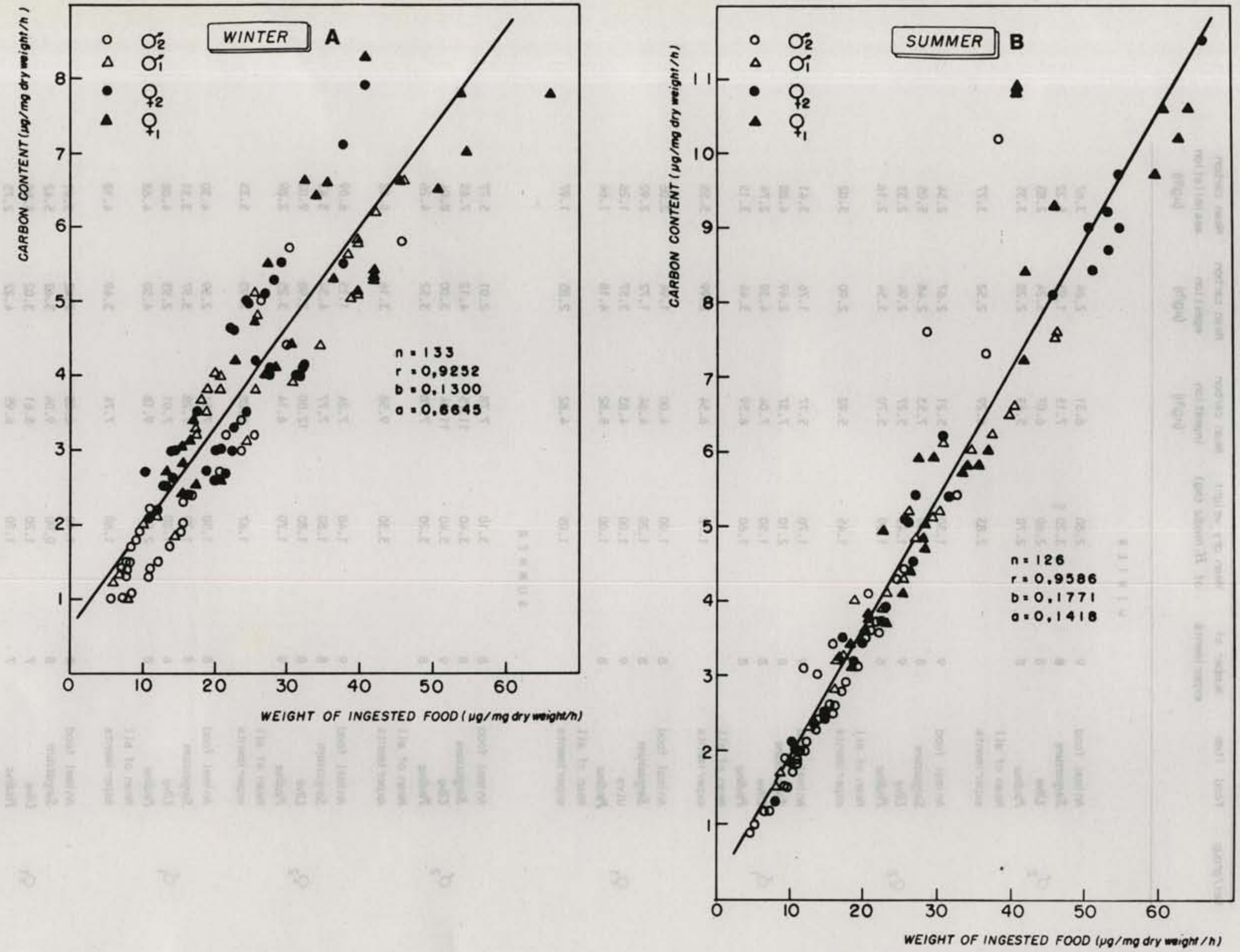

Fig. 1. Relationship between the weight of the food ingested and the carbon content of an equal weight of the same food item ingested by *Hyale media* in winter (a) and summer (b).

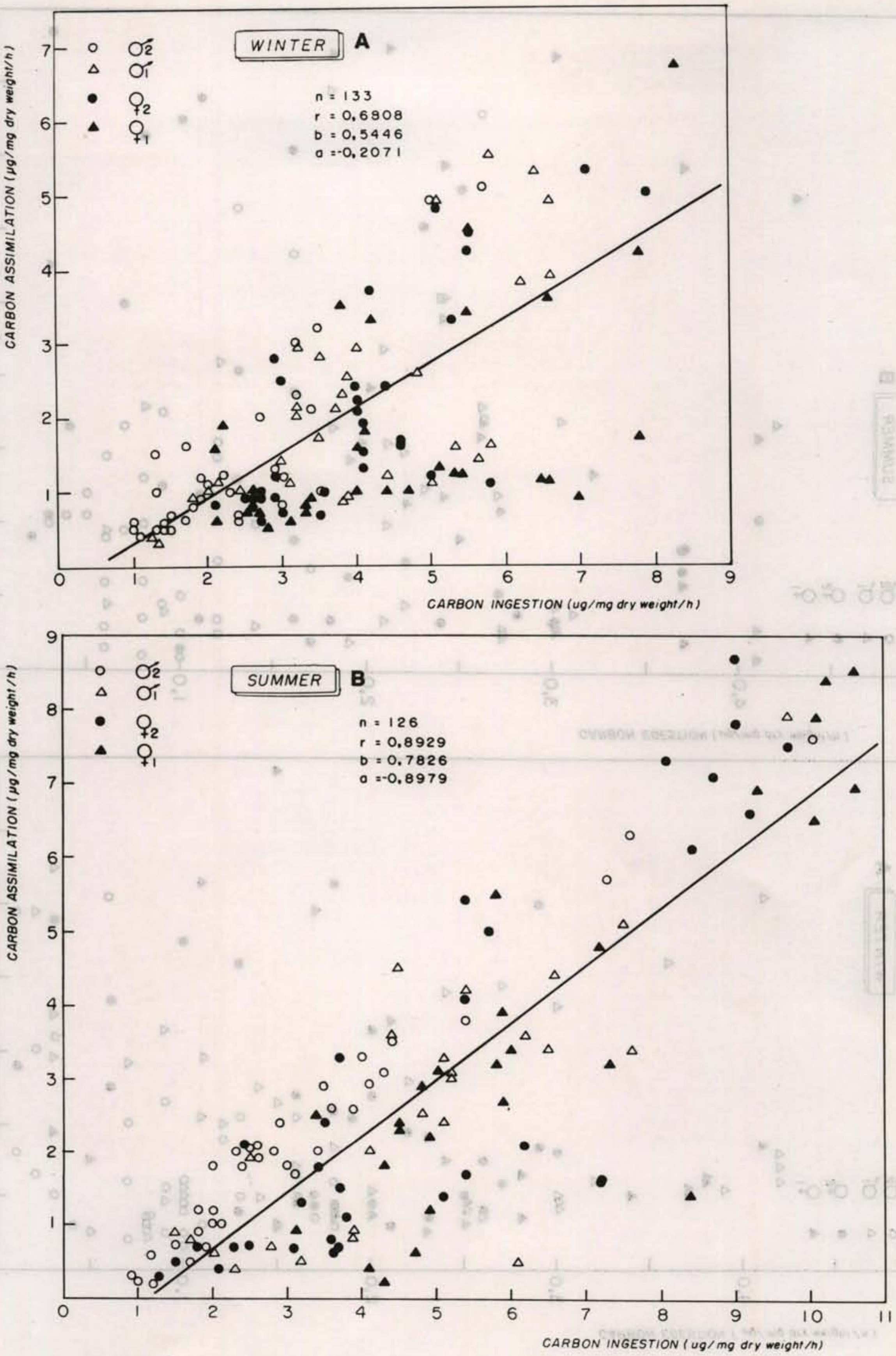

Fig. 2. Relationship between carbon ingestion and carbon assimilation rates in winter (a) and summer (b).

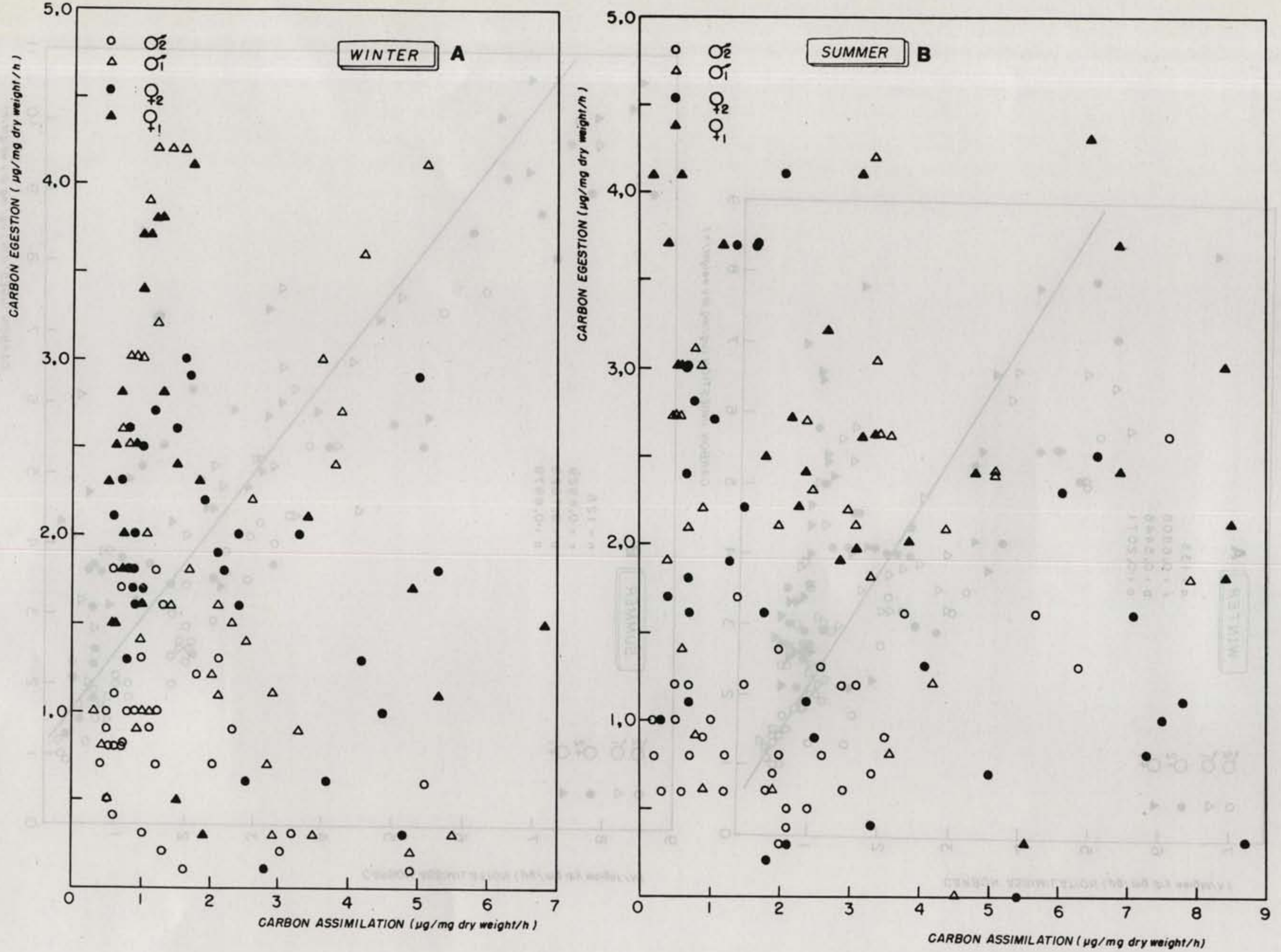

Fig. 3. Relationship between carbon assimilation and carbon egestion rates in winter (a) and summer (b).

in their food preferences, in order to balance their requirements for survival, growth speed, moulting, maturity and longevity. Since only two experimental temperatures were used here, the actual effects of temperature on the feeding rates of *H. media* could not be analyzed.

In winter temperatures, the development and sexual stages of *Hyale media* did not show any particular food "preference" (ANOVA, $p > 0.05$). However, in summer temperatures, (♀$_1$ had higher assimilation rates for *Sargassum* and *Ulva*, and ♀$_2$ for animal food and *Ulva* (ANOVA, $p \leq 0.05$).

No studies on the seasonality of the algal food items used, in the region from where the specimens of *Hyale* were collected, have been undertaken to this date. Animal food, *Ericthonius brasiliensis* is known to occur during summer and winter time (Wakabara *et al.*, 1983). Nevertheless, it seems that the food items utilized in this work are found in the *H. media* sampling site throughout the year. Considering that the seasonal temperature, variation in the studied area is not large, it is unlikely that the choice of a food item would be determined by the absence of certain organisms or unsuitability of others due to variations in their biochemical or energetic characteristics. Temperature variation might affect the metabolism or the physiological characteristics of *Hyale* and these are the determinants of food choice.

A type of food may be ingested because it promotes rapid growth, early maturation and greatest survival of the younger, or longevity of the species. Animal food is apparently required by *Gammarus lawrencianus* for rapid growth and early maturation, however fine algae were found to be important for the greater survival of the young (Vassalo & Steele, 1980). Willoughby & Sutcliffe (1976) verified that the rate of moulting and changes in the body weight of *G. pulex* at a single temperature reflected the varying nutritional values of different types of diet. Animal food generally contains a large proportion of usable organic material in comparison with plant food, and hence, carnivores would be expected to have higher assimilation efficiences than herbivores. In predaceous animals, food assimilation is very high. *Ulva* should be rewarding as a food source, since it has the greater number of calories.g^{-1} amongst 14 seaweeds studied (Carefoot, 1973).

Prus (1971) working with the Isopoda *Asellus aquaticus* argues that ovigerous females have high assimilation efficiency to balance the energy and material needed in this stage, without any increase in food intake. In this study account, in summer, *Hyale* ovigerous females as well as males 2 have also shown the highest assimilation efficiencies. However, mean assimilation rates resulted from an increase in food ingestion in relation to winter, for mean egestion rates did not show significant variation from winter to summer. The discrepancy found in relation to Prus work may be explained, amongst other causes, by the fact that *Hyale* ♀$_2$ may actually pass through many different physiological phases. In antenna 1 of ♀$_2$ there are 11 or 12 articles. According to Leite (1976) *Hyale* females with 11 or 12 articles in the antenna show slight morphological differences among them. At this stage *Hyale* females are fertilized between moultings and their growth rate is slower than that in the other stages. On the other hand, females have no physiological resting periods. After the young are released, females moult again and are fertilized.

Steele (1973) found that females of *Parhyalella pietchmanni* with embryos in the brood pouch, already had mature ovaries. The grows rate of *Hyale* ovigerous females is largely reduced or abolished, after reaching sexual maturity, while males go on growing. This may explain why ♂$_2$, in this work have a high assimilation efficiency both in winter and in summer while ♀$_2$ have low and high assimilation efficiency respectively in winter and summer. In ovigerous females the variability of the assimilation efficiency may depend upon the egg-embryo development, more than on the growth rate. As egg-embryo development time depends amongst other factors, upon temperature, *H. media* develops more rapidly in summer than in winter, and females, having no sexual resting time, are fertilized more often than in winter. In consequence ovigerous females represent a physiological state greatly enhanced by sexual hormones, which affects greatly some aspects of feeding rates and assimilation efficiency.

The Prus (1971), assertion that females do not feed during the reproductive stage is partially true for *Hyale media,* if one considers that the females have no sexual resting period. However, it should be pointed out that ovigerous females have to provide material and energy for egg development at least until the eggs are released in the brood pouch.

Resumo

No presente estudo foram analisados em laboratório, sob temperaturas de inverno e verão, aspectos quantitativos da alimentação de *Hyale media* (Crustacea-Amphipoda), utilizando-se o método gravimétrico, aliado ao conteúdo de carbono dos itens alimentares oferecidos.

Nos experimentos com temperatura de inverno não foi encontrado diferença significativa nas taxas de assimilação entre os diferentes estádios de desenvolvimento e sexo. Naqueles com temperatura de verão as taxas de assimilação para fêmeas ovígera e não ovígera foram maiores que aquelas encontradas para machos adulto e jovem.

As variações encontradas nas taxa e eficiência de assimilação foram explicadas pelo efeito diferencial da temperatura sobre a taxa de crescimento específico e condições fisiológicas de cada estádio de desenvolvimento.

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