

Ecological energetics of *Chaoborus* in a tropical lake

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Summary. Ecological energetics of *Chaoborus brasiliensis* from Lake Valencia, Venezuela, were studied between February 1979 and February 1980. Direct measurements were made of the respiration rate, assimilation efficiency, and growth rate of all 4 larval instars and of the pupae. For the larval stages, respiration increased as the 0.67 power of body mass. Respiration rates of the larvae, when corrected for body size and temperature, were extraordinarily low by comparison with the rates for most aquatic insects. The respiration rates of pupae were 3 times as high as those of larvae the same size. Assimilation rates increased significantly with body size for the larvae and differed slightly but significantly among food types. Assimilation efficiencies fell within the expected range for carnivores. The growth efficiencies were exceptionally high for instars II-IV by comparison with other small aquatic organisms. High growth efficiency for *Chaoborus brasiliensis*, and possibly for *Chaoborus* generally, is explained by a very low maintenance cost and may be a significant explanation for the wide distribution and high degree of ecological success in this primary carnivore of plankton communities.

Key words: Zooplankton Energetics – Predation – Assimilation – Respiration

A complete understanding of the factors that regulate populations and communities cannot be achieved without information on the energetics of individual organisms. Analysis of the energy budgets may reveal substantial differences in the costs of organism maintenance and in the efficiency of food utilization, and may thus contribute to explanations of the distribution and abundance of a species and of its role within a community. While these principles have been understood by ecologists for many years, detailed studies of ecological energetics in relation to populations in the field are still surprisingly few (Grodzinski et al. 1975).

We give here an analysis of the energetics of *Chaoborus brasiliensis* from Lake Valencia, Venezuela. The analysis has a dual purpose. First, since *Chaoborus* is the most important primary carnivore in the plankton of Lake Valencia, its energy allocation is important to the Lake Valencia ecosystem, which was studied intensively between 1976 and 1981 (Lewis 1986). In addition, we wish to test the hypothesis that the extraordinary worldwide success of *Chaoborus* as

a primary carnivore in the plankton environment of lakes is explained to a significant degree by exceptionally high efficiency in the use of energy.

Ecological energetics has been studied for several temperate species of *Chaoborus* (Sigmon et al. 1978; Swift 1976; Giguère 1980). This information will provide some useful comparisons for *Chaoborus* of Lake Valencia. Although some of the previous studies are detailed in their coverage of the terms in the energy budget, all previous studies have focused specifically on the largest *Chaoborus* larvae (primarily instar IV). Since the energy budget of any species may change considerably during development, we have included in the Lake Valencia studies larvae of all four larval instars plus the pupae of *Chaoborus*. This gives a broader perspective on the energetics of the entire life cycle.

Chaoborus brasiliensis is a small *Chaoborus* species (0.8 cm maximum length for larvae). Since the herbivores in the zooplankton of Lake Valencia are relatively small also, however, the larger instars of *C. brasiliensis* can consume all species of zooplankton herbivores in Lake Valencia. Common food items include rotifers, cladocerans, cyclopoid copepods, and calanoid copepods (Saunders 1980). The smallest *Chaoborus* larvae can feed only on the smallest herbivores. Diet breadth increases with age to include not only the smallest herbivores but also the larger copepod stages and cladocerans. In Lake Valencia, *C. brasiliensis*, which is the only species of *Chaoborus* present in the lake, has a major effect on the planktonic food web. The mean population density of larvae is approximately 30,000 organisms per m², which is sufficient to exert great predation pressure on planktonic herbivores (Cressa 1985).

Lake Valencia is located in north central Venezuela (10°10'N, 68°25'E). The lake has an elevation of 404 m ASL, a surface area of 351 km², and a maximum depth of 39 m. Lake Valencia is eutrophic, and consequently supports large populations of planktonic algae (ca. 40 µg/l chlorophyll a). The water column is principally unstratified during the dry season (usually December through April) and is stratified during the remainder of the year (Lewis 1983, 1984). During the stratification period, the upper mixed layer has an average depth of 13 m. *Chaoborus* larvae are present in the lake throughout the year, but are especially abundant during the period of stratification.

Methods

All of the work was conducted between February 1979 and May 1980. Animals that were used in laboratory experiments were in all instances obtained directly from Lake Valencia, and the experiments were conducted at a labora-

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tory near the lake. The animals were always held in water from Lake Valencia and were fed with plankton from Lake Valencia.

Items in the energy budget of any organism include growth (here symbolized as production, P), consumption (C), respiration (R), excretion (U), and fecal output (F). Assimilation (A) is estimated as the sum of respiration and production. Ratios of interest include assimilation efficiency (AE), which is taken as $(R + P)/C$. The gross growth efficiency (K_1) is the portion of consumption that goes into growth (P/C), and the net growth efficiency (K_2) is the portion of assimilation that goes into growth (P/A).

Production, respiration, and assimilation efficiency were determined directly by methods described below. Consumption was computed as the ratio of assimilation to assimilation efficiency. Urinary output was assumed on the basis of the literature (Swift 1976; Tudorancea et al. 1979) to be negligible. Fecal output was not measured. Biomass was converted to energy on the basis of 4.936 cal/mg dry weight (Jonasson 1972); 1 μ l of O_2 was assumed to equal 0.0048 cal (Peters 1983). The dry weights of individual *Chaoborus* were determined on the basis of equations relating head size or body size to dry weight specifically for the Lake Valencia population of *C. brasiliensis*, as described in Cressa and Lewis (1984).

Respiration was determined by the oxygen-difference method for each larval instar and for the pupae of *Chaoborus*. The organisms were collected at dawn with a plankton net, and were transported to the laboratory where they were sorted according to instar and transferred to a container where they were kept without food for 24 h. Individuals of instar I were obtained by hatching eggs of *Chaoborus* in the laboratory.

At the beginning of each respiration experiment, organisms of a given instar were transferred to a bottle containing 25 ml of lake water. The numbers of individuals per bottle varied by instar as follows: I or II, 20; III or IV, 10; pupae, 5. The lake water was filtered through glass-fiber paper (Whatman GF/C) and was saturated with oxygen prior to being used in the experiments. Experiments on individual instars were always run in quadruplicate and all experiments were accompanied by triplicate blanks consisting of filtered lake water enclosed in bottles to which no *Chaoborus* larvae were added. Analysis of the blanks consistently showed negligible oxygen demand and low variation among blanks, indicating that the preparation of the water was adequate to insure uniform oxygen concentrations and low intrinsic oxygen demand.

In all of the experiments, respiration was determined at 26° C. Lake Valencia has an average temperature of 27° C and varies no more than 2° C to either side of this average through time or depth (Lewis 1984). The duration of the incubations in all cases was 24 h. Oxygen determinations on water from each bottle were made in duplicate by Winkler titration at the end of each experiment. Titrations were accomplished with a micrometer buret on a 10-ml sample volume.

Assimilation efficiency was determined with sulfur-35 by a method similar to the one described by Frost (1980). As in the respiration experiments, *Chaoborus* larvae from Lake Valencia were acclimated in the laboratory without food for 24 h. Zooplankton herbivores were also removed from Lake Valencia prior to each experiment and were allowed to feed on yeast that had been labeled with sulfur-35.

Table 1. Instantaneous growth rate (% per day), standard body length (i.e., length between air bladders, which is close to 0.5 times total length), and weight for the larval instars of *Chaoborus brasiliensis*

Instar	Standard length (μ m)	Dry weight (μ g)	Development time (days)	Growth rate (%/day)
I	877–1,023	1.29– 2.15	5.1	9.9
II	1,023–2,000	2.15– 17.0	7.6	27.2
III	2,000–2,800	17.0 – 50.0	11.3	9.5
IV	2,800–4,000	50.0 –190.0	13.6	9.8

Labeled zooplankton were transferred to a container lacking sulfur-35, and were allowed to remain for one hour, thus releasing unassimilated sulfur-35 label. Individuals of desired prey types were selected from these protoplasmically-labeled herbivores. Prey types that were used in the experiments were *Brachionus calyciflorus*, *Ceriodaphnia cornuta*, and *Moina micrura*. The radioactivity of food items was for each experiment determined by the analysis of 10 of the labeled prey; there were always 5 replicates of these determinations. The prey items used for this purpose were transferred to Millipore filters (0.45 μ m pore size) and dried for 24 h at 60° C. After this, they were digested with a mixture of $HClO_4$ and H_2O_2 (1:1) and dried in an oven for 45 min. The samples were allowed to cool for 10 to 20 min, after which scintillation cocktail was added. The amount of sulfur-35 was then determined with a scintillation counter. From the results of the scintillation counting, corrected for background and for counting efficiency, calculations were made of the average disintegrations per min (dpm) per prey item for a particular sample.

For the assimilation experiments, two *Chaoborus* of the same instar were transferred to a 50-ml jar and were offered the labeled prey (20 *Brachionus*; 10 *Ceriodaphnia* or *Moina*). The *Chaoborus* were allowed 24 h for feeding. The larvae were then transferred to another jar containing filtered water and were held for 6 h. They were then killed with buffered formalin, their size was determined, and the amount of sulfur-35 in each larva was obtained by scintillation counting. A determination was made of the number of prey that had been eaten (typically all prey were eaten). The assimilation efficiency was then computed as the observed dpm in the larvae in relation to the dpm in the prey.

Growth (production) was determined from a combination of field and laboratory data. Pupal development was determined under laboratory conditions. It was not possible to rear the larval stages in the laboratory. However, Saunders (1980) conducted an extensive study of larval development under field conditions using cohort analysis. The cohort analysis of Saunders gives development rates that are near the maximum rates because the recognizable cohorts occur during intervals when the growth conditions are most favorable for *Chaoborus*.

Results

Table 1 gives the development times for each of the instars and the corresponding weight ranges and instantaneous percent growth per day (computed on an exponential basis).

Table 2. Mean oxygen consumption rates for *Chaoborus* and comparative values from the literature. All values were converted to 26 C by means of Winberg's correction coefficient (Grodzinski et al. 1975). Values in parentheses represent the oxygen consumption of *C. brasiliensis* at a body mass equal to that of the species indicated

Species	Stage	Dry weight (μg)	Oxygen consumption		Source
			$\mu\text{l org}^{-1} \text{h}^{-1}$	$\mu\text{l mg}^{-1} \text{h}^{-1}$	
<i>C. brasiliensis</i>	I	1.8	0.013	6.35	This study
	II	5.4	0.021	4.35	
	III	20.5	0.053	2.80	
	IV	184.3	0.259	1.36	
	Pupae	210.3	0.654	3.13	
<i>C. trivittatus</i>	Young IV	1,300	1.07 (0.97)	0.82 ^a (0.71)	Giguere (1980)
	Old IV	1,840	1.65 (1.22)	0.90 ^a (0.63)	
<i>C. trivittatus</i>	Young IV	–	1.02	2.23	Swift (1976)
	Old IV	–	2.16	1.46	
<i>C. punctipennis</i>	IV	310 ^b	2.60 ^a (0.37)	8.40 ^a (1.14)	Sigmon et al. (1978)
<i>C. spp.</i> ^c	III + IV	–	0.21	2.38	Alvarez (1971)
	Pupae	–	0.77	4.81	

^a Recalculated from data given by the author

^b Juday (1921)

^c *C. brasiliensis* and *C. magnificus*

Table 3. Assimilation efficiencies for *Chaoborus brasiliensis* from Lake Valencia and for other species of *Chaoborus* in relation to temperature and prey type

Species	Temperature (° C)	Prey Species	Meal size		Assimilation efficiency	
			Length (mm)	Volume (μl)		
Lake Valencia	<i>C. brasiliensis</i> (IV)	26	<i>Moina micrura</i>	0.45	0.010	0.57
			<i>Ceriodaphnia cornuta</i>	0.39	0.007	0.61
			<i>Brachionus calyciflorus</i>	0.25	0.002	0.65
			<i>B. calyciflorus</i>	0.25	0.002	0.59
Other Sources	<i>C. brasiliensis</i> (III)	26	<i>B. calyciflorus</i>	0.25	0.002	0.59
		26	<i>B. calyciflorus</i>	0.25	0.002	0.54
	<i>C. trivittatus</i> (IV) ^a	15	<i>Diaptomus kenai</i>	–	–	0.76
			<i>Daphnia magna</i>	–	–	0.62
			<i>Diaptomus kenai</i>	1.3	0.2	0.91
	<i>C. trivittatus</i> (IV) ^b	16		1.8	0.3	0.90
				2.2	0.5	0.85
					0.2–0.8	0.80
		24		0.2	0.87	
		6		0.4	0.88	
			0.5	0.87		
			0.9	0.52		

^a Swift (1976)

^b Giguère (1981)

The pupae, which do not grow, have a development time of 2 days. The growth of larvae is most rapid in instar II. The total estimated life cycle time, which is 43 days under good growing conditions (with allowances for egg laying and hatching), is in good agreement with the few reported values for tropical species (MacDonald 1956; Cressa 1971; Lewis 1979).

Figure 1 shows the results of the respiration studies on larvae. On a logarithmic basis, oxygen consumption per larva increases in a smooth, linear manner as a function of increasing weight. Regression analysis shows that $\log(\text{nl O}_2 \text{ consumed per organism per h}) = 0.67 \log(\text{dry mass in ng}) - 1.11$ and that $\log(\text{nl O}_2 \text{ consumed per gram dry mass per h}) = -0.33 \log(\text{dry mass in ng}) + 1.87$. The standard error of the slope for both equations is 0.01.

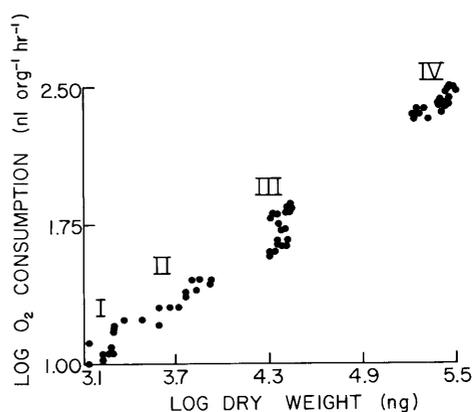


Fig. 1. Respiration rates of *Chaoborus brasiliensis*

Table 4. Composite assimilation efficiencies, consumption, and growth efficiencies for *Chaoborus brasiliensis*

Instar	Assimilation Efficiencies	C % of body weight/day	P/C (K ₁)	P/A (K ₂)
I	0.54	46	0.22	0.40
II	0.54	69	0.39	0.73
III	0.59	27	0.35	0.59
IV	0.61	21	0.46	0.76

Table 2 shows the average respiration rates per organism and per unit weight for experimental organisms within each instar, and also provides comparable data from the literature for other species of *Chaoborus*. All of the data from the literature are corrected to a common temperature of 26° C in order to facilitate comparisons. In three cases from the literature, the weights of the larvae used in experiments were reported, and in these instances it is possible to calculate from the relationship between mass and respiration rate what the respiration rate would be for *C. brasiliensis* of identical size to the organism on which experiments were done. These values are shown in parentheses in Table 2.

As shown by Table 2, oxygen consumption per unit weight decreases steadily from smaller to larger instars for larvae. However, the metabolic rate per unit weight for pupae is approximately three times as high as would be expected on the basis of their size.

Table 3 summarizes the data on assimilation efficiency of instars II through IV of *C. brasiliensis*. It was not possible to obtain measurements for instar I because the instar I larvae did not feed readily. Consequently, computations involving assimilation efficiency for instar I are made using the data for instar II.

Despite the great range in size among the three instars that were tested, it was possible to obtain measurements of assimilation efficiency for the same prey type (*Brachionus calyciflorus*) on all three instars. The data shown in Table 3 suggest that the assimilation efficiency increases as the larvae become older. This is confirmed by analysis of variance, which shows a significant difference among mean assimilation efficiencies of the instars ($p < 0.05$). Table 3 also indicates a difference in assimilation efficiencies across prey types, (analysis of variance, $p < 0.05$). Assimilation efficiency is highest for *Brachionus*, lower for *Ceriodaphnia*, and still lower for *Moina*.

Table 3 shows the assimilation efficiencies reported in the literature for *Chaoborus*. The efficiencies of the different species overlap. The values obtained by Giguère (1980) for *C. trivittatus* are the highest in most instances, but different prey types were used and this may be partially responsible for differing assimilation efficiencies.

Table 4 gives the consumption as calculated from assimilation and growth, and shows the growth efficiencies K₁ and K₂.

Discussion

It is well known that the slope of a line relating metabolism per organism to the logarithm of body mass is close to 0.75 over large size ranges of organisms (Peters 1983). For

aquatic invertebrates generally, the slope may even be slightly higher (Lampert 1984). Deviations from the general slope may apply over smaller size ranges of organisms, or across the developmental range within the life history of a given organism. The respiration data for *C. brasiliensis* in Lake Valencia conform fairly closely to the general size-metabolism relationship, but the slope is somewhat lower, and would thus correspond to a slower increase of respiration with size than is usually expected.

The respiration data provide a means of testing the hypothesis that *Chaoborus* is exceptionally efficient in its use of energy. Table 5 shows the respiration rates of aquatic insects as obtained from the literature. All of the rates are corrected to a common temperature of 26° C, and in all instances the table shows the calculated equivalent metabolism for *C. brasiliensis* of the same size as the indicated organism. The table shows that *C. brasiliensis* is more similar in its metabolism to other species of *Chaoborus* than it is to other aquatic insects, which typically have metabolic rates several times higher than *C. brasiliensis*. Thus, when corrections are made for size and for temperature, *C. brasiliensis* and probably *Chaoborus* in general are distinctive among aquatic Insecta in having especially low energy demands for maintenance. Although the behavioral, physical, or physiological mechanisms that explain the low maintenance requirements of *Chaoborus* are not clear, they could involve such adaptations as the ambush mode of feeding, which requires minimal activity, and the ingestion of whole food items, which precludes the need for certain types of food processing.

The metabolic rate per unit weight for *Chaoborus* pupae substantially exceeds the rate that would be expected from extrapolation of the relationship between size and metabolic rate for larvae. It seems reasonable to conclude that the higher metabolic rate in pupae is explained by the rapid metamorphosis of tissues that occurs during pupation. Because the duration of the pupal stage is known, as is the metabolic rate during pupation, it is possible to compute an ecological cost for metamorphosis in *C. brasiliensis*.

The period of pupation lasts 2.0 days, during which there is no growth. Furthermore, since there is a steady and relatively high respiratory demand during pupation, a certain amount of the growth that occurs during larval stages can be attributed to the energy requirements of pupation. It can be calculated from the instantaneous growth rate of the instar IV larvae, the respiration rate of the pupae, and the size range of the instar IV larvae that the last 1.9 days of instar IV larval growth are required to add the biomass that is in turn used to supply the respiration energy for pupation. Thus the total cost for pupation is 2.0 days for the pupal stage itself plus 1.9 days of larval growth required to add the biomass that is used up during pupation. In terms of biomass growth, the pupation phase decreases the overall instantaneous growth rate from 0.0177 per day to 0.0161 per day. Thus 9% is the energetic cost of pupation in *C. brasiliensis*.

The literature on invertebrates indicates that younger instars typically have a higher assimilation efficiency than older ones (Lawton 1970; Grodzinski et al. 1975). This is not true of *Chaoborus brasiliensis*, as shown by Table 3. Differences in assimilation efficiency of *Chaoborus* and other invertebrates in this respect may be explained by the peculiar mode of feeding of *Chaoborus*. *Chaoborus* ingests its food whole, retains the food in a crop where the fluid

Table 5. Respiration rates for aquatic insects. The reported values were converted to 26° C by means of Winberg's correction coefficient (Grodzinski et al. 1975). Values in parentheses represent oxygen consumption of *Chaoborus brasiliensis* corrected for weight differences

Species	Dry weight (mg)	Respiration		Source
		$\mu\text{l org}^{-1}\text{h}^{-1}$	$\mu\text{l mg}^{-1}\text{h}^{-1}$	
Plecoptera				
<i>Perlodes intricata</i>	100.00	21.55 (17.80)	0.22 (0.18)	Grodzinski et al. (1975)
<i>Isoperla buresi</i>	5.34	8.61 (2.50)	1.61 (0.47)	Kamler (1969)
Ephemeroptera				
<i>Cloeon dipterum</i>	0.22	0.93 (0.29)	4.23 (1.32)	Kamler (1969)
<i>Stenonema pulchellum</i>	2.00	5.71 (1.29)	2.86 (0.65)	Trama (1972)
<i>Ecdyonurus venosus</i>	5.50	34.10 (2.55)	6.20 (0.46)	Ambuhl (1959)
Diptera				
<i>Chironomus anthracinus</i>	8.00	4.49 (3.27)	0.56 (0.41)	Berg et al. (1962)
<i>Chironomus strenzkei</i>	0.38	1.80 (0.43)	4.75 (1.12)	Platzer-Schultz (1970)
<i>Chaoborus trivittatus</i>	1.84	1.65 (1.23)	0.90 (0.67)	Giguère (1980)
<i>Chaoborus flavicans</i>	5.00	5.83 (2.39)	1.17 (0.48)	Berg et al. (1962)
<i>Chaoborus brasiliensis</i>	0.18	0.26	1.44	This study

and solid portions become separated, and periodically empties the crop of solid fragments. Small organisms may lose more nutritive fluids when the crop is emptied.

The assimilation efficiencies for *C. brasiliensis* fall within the range of most common values reported by Grodzinski et al. (1975) for invertebrate predators (0.50–0.66). As expected, the assimilation efficiencies for *C. brasiliensis* are higher than for invertebrate herbivores (0.37–0.40) or detritivores (0.22–0.27). The assimilation efficiencies are lower for *C. brasiliensis* than for *C. trivittatus*. This difference may be attributable to the much larger prey sizes taken by *C. trivittatus*; larger prey are likely to have a lower percentage of skeletal material in the biomass.

The values of K_1 and K_2 are lower for instars I and III of *C. brasiliensis* than for the other two instars (Table 4). As we have noted in a previous study (Cressa and Lewis 1984), *C. brasiliensis* shows very uneven change in weight across the 4 instars; very little growth occurs in instar I, while exceptionally rapid growth occurs in instar II. We have postulated that instar I is principally devoted to tissue organization, which is followed by growth in instar II. The sequence is repeated, but in a less exaggerated way, between instars III and IV. Diversion of large amounts of energy to tissue differentiation in instars I and III would account for the low K_2 values of these instars by comparison with other instars.

The values of K_1 and K_2 are also relevant to the hypothesis that *Chaoborus* has an exceptionally high efficiency of energy use. Table 6 compares the K_1 and K_2 values of *Chaoborus* with those of other aquatic Crustacea and Insecta. With the exception of instar I, both the K_1 and K_2 values of *Chaoborus* are high by comparison with those of aquatic herbivores and detritivores. The K_1 values of *Chaoborus* are most similar to those of other carnivores and, for instars II–IV, the K_2 values are higher than the K_2 values of other carnivores. The most similar value among the carnivores. The most similar value among the carnivores shown in Table 6 is for *Lestes sponsa*, which, like *Chaoborus*, is an ambush predator. The high values of K_2 reflect mostly the low respiration rate of *Chaoborus*, which allows an exceptionally high proportion of assimilation to be diverted into increased body mass.

Both the respiration data and the K_1 and K_2 ratios

Table 6. Ecological efficiencies of small aquatic organism

Taxon	K_1	K_2	AE	Source
Herbivores				
<i>Brachionus calyciflorus</i>	0.19–0.36	0.47–0.69	0.40–0.52	Galkovskaya (1963)
<i>B. plicatilis</i>	0.11	0.57	0.19	Doohan (1973)
<i>Eudiaptomus gracilis</i>	0.06–0.32	0.18–0.53	0.33–0.59	Kibby (1971)
Detritivores				
<i>Harnischia curtilamellata</i>	0.20	0.25	0.80	Tudorancea et al. (1979)
<i>Chironomus</i> sp.	0.36	0.45	0.80	Tudorancea et al. (1979)
Carnivores				
<i>Procladius freemani</i>	0.13	0.16	0.81	Tudorancea et al. (1979)
<i>Lestes sponsa</i>	0.19	0.64	0.20–0.40	Lawton (1970)
<i>Pyrrhosoma nymphula</i>	0.42–0.45	0.50	0.86	Lawton (1970)
<i>Macrocyclops albidus</i>	0.20–0.50	0.45–0.55	0.44–0.91	Klekowski (1970)
<i>Chaoborus trivittatus</i> IV ^a	–	–	0.87	Giguère (1981)
<i>C. trivittatus</i> IV ^a	–	–	0.69	Swift (1976)
<i>C. brasiliensis</i>				
I	0.22	0.40	0.54	This study
II	0.39	0.73	0.54	
III	0.35	0.59	0.59	
IV	0.46	0.76	0.61	

^a Median from Table 3

derived from assimilation data tend to confirm the hypothesis that the widespread occurrence of *Chaoborus* and the ability of *Chaoborus* to dominate the primary carnivore level of many plankton environments such as that of Lake Valencia is in part explained by extraordinary energy efficiency, and particularly the high proportion of assimilated energy that can be diverted into growth.

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