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Trophic Ecology of *Hyalella* Sp (Crustácea: Amphipoda) in a High Andes Headwater River with Travertine Deposits

Key words: Hyalella, Amphipoda, Andes, tropical streams, travertine, shredders

Abstract

We studied the diet of 50 specimens of *Hyalella* sp. collected in the karstic headwaters of a high-altitude Andean river (3817 m a.s.l. Peru) in four different habitats: macrophytes, bryophytes, leaf litter, and layers of travertine. The gut content analysis showed a dominance of fine particulate organic matter (FPOM) in most habitats—layers of travertine (69.5%), *Myriophylum* (58.5%) and bryophytes (56.8%)—except for individuals collected in leaf litter where coarse particulate organic matter (CPOM) represented 68%of gut content, which indicates a high trophic flexibility of *Hyalella* sp. Likewise, in an experiment with feeding chambers *in situ* during three days, twenty individuals of *Hyalella* sp. presented a higher consumption of leaf litter of native species (*Polylepis* sp.) (0.025 mg/day) than those of an introduced species (*Eucalyptus globulus*) (0.008 mg/day).

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1. Introduction

The input and decomposition of allochthonous organic matter is considered an important energy source in rivers with forested riparian zones and determine the diversity and abundance of trophic functional groups in these ecosystems (PETERSEN and CUMMINS, 1974; GRAÇA, 2001). Downstream processing of coarse particulate organic matter (CPOM) from the riparian vegetation into fine particulate organic matter (FPOM) is carried out by a number of abiotic and biotic factors among which, the activity of shredders is recognized as the first link in the food chain in river headwaters (VANNOTE *et al*., 1980; WEBSTER and BENFIELD, 1986; GRAÇA, 1993; WALLACE *et al*., 1997; GRAÇA, 2001).

The preference for a species of leaf litter by a shredder depends on several factors: leaf toughness, leaf conditioning status, concentration of nutrients and presence of secondary metabolites that may diminish the palatability of leaves to herbivores (WEBSTER and BENFIELD, 1983; YEATES and BARMUTA, 1999; GRAÇA, 2001; GRAÇA *et al*., 2001; GRAÇA and CRESSA 2010). For example, RINCÓN and MARTÍNEZ (2006) determined experimentally that *Phylloicus* (Calamoceratidae) preferred to feed on *Ficus* leaves, that have high nutrient contents and low concentrations of structural compounds (such as lignin and cellulose) but rejected *Anacardium* leaves, which has high concentrations of chemical defences such as polyphenolics (tannins). Likewise, GRAÇA *et al*. (2001) working with tropical and template leaf litter, reported that feeding preferences, survival and growth rate of two tropical shredders (*Nectopsyche argentata* and *Phylloicus priapulus*) did no depend as much on the geographical origin of the leaf as it does on other factors as food quality and previous conditioning. In this context, *Eucalyptus globulus* leaves, exotic specie frequently introduced in tropical high Andean, has been mentioned as of low nutritive quality, slow breakdown rate, high toughness and content of phenolics and tannins (BUNN, 1988; BOULTON, 1991; CANHOTO and GRAÇA, 1995; ABELHO & GRAÇA, 1996). Recently RATNARAJAH and BARMUTA (2009) reported that in Australia the amphipod *Antipodeus wellingtoni* showed a clear preference for *E. globulus*. Due to this, other factors should be influencing this trend. Presumably some invertebrates in Australian streams have mechanisms that allow them either to avoid or to process polyphenolic and other plant defensive compounds (CAMPBELL and FUCHSHUBER, 1994).

Although in temperate rivers an increase in shredder density has traditionally been associated with the seasonal input of allochthonous material during autumn (PETERSEN and CUMMINS, 1974 WEBSTER and BENFIELD, 1986), in tropical rivers, with a lack of seasonality of litterfall, the predictability of the detrital food is reduced (COVICH, 1988). Likewise, many families of Plecoptera and Trichoptera, frequently considered as typical shredders from temperate streams are apparently largely missing in tropical streams (WANTZEN and WAGNER, 2006). Due to this, the importance of macroinvertebrates shredders in the processing of particulate organic matter in tropical streams has been questioned (LINKLATER, 1995; BENSTEAD, 1996; DUDGEON and WU, 1999; DOBSON *et al*., 2002; MATHURIAU and CHAUVET, 2002; WANTZEN and WAGNER, 2006; JACOBSEN, 2008). For example, MATHURIAU *et al*. (2008) suggested in a tropical stream in Colombia, that shredders appear to have a minor role in the decomposition of organic matter due to strong variability of discharge and its influence on leaf litter retention. On the other hand, several studies support that in tropical rivers, shredders are not important since microbial processing is more active in the tropics that in temperate regions, e.g. IRONS *et al*. (1994). Likewise, other works have reported that some macroconsumers may occupy the shredder feeding niche. ROSEMOND *et al.* (1998) working in Costa Rica, showed that fishes and shrimps may be very important in processing organic matter and play an analogous role to small insects shredders in temperate streams. Similar results have been observed with crabs in Kenya (DOBSON et *al*., 2002), crayfish in Australia (BOYERO *et al*., 2007) and snails and semi-terrestrial cockroaches in Malaysia (YULE *et al*., 2009)

In contrast, some studies have reported the importance of activity macroinvertebrate shredders in tropical streams (YULE, 1996; CHESHIRE *et al*., 2005; BOYERO *et al.*, 2006; CHARA *et al*., 2007; RÍOS *et al*., 2009; YULE *et al*., 2009). In this context, TOMANOVA *et al*. (2006) and CAMACHO *et al.* (2009) indicated that its function has been underestimated due to the assumption that belong to the same taxa that in temperate river and that gut content analysis is necessary for to assign real functional feeding groups to the tropical macroinvertebrates. For example, in Australian streams, CHESHIRE *et al*. (2005) based on gut contents analysis, found that despite of many invertebrates were generalist in their diets, shredders were an important component of the assemblages, especially in biomass and richness taxa. Also, CHARA *et al*. (2007) evaluated the decomposition of three native plant species in a river headwater in the Colombian Andes indicating that shredders represent an important role in litter breakdown. Furthermore, RÍOS *et al.* (2009) reported a shredder activity of 35% (by gut content analysis) on the basis of the relative density of 11 most abundant taxa in a river headwater in the highlands of Ecuador.

Amphipods are one of the groups commonly known as macroinvertebrate shredders in temperate rivers (CUMMINS and KLUG, 1979; TACHET *et al*., 2000) and are considered important in the incorporation of energy from streamside vegetation into the food web of rivers (WALLACE *et al*., 1997; GRAÇA *et al*., 2001). They are associated with different types of microhabitats, representing a significant part of the benthic biomass in both lentic and lotic environments around the world (WEN, 1992; CASSET *et al*., 2001), and in some cases constitute up to 20% of the total community abundance (e.g. in Lake Titicaca: DEJOUX, 1991). While in Europe the genus *Gammarus* is common, in South America *Hyalella* is the only epigeal genus of Amphipoda with approximately 50 species described, although the true richness of species is still unknown (VÄINÖLÄ *et al*., 2008; PERALTA and GROSSO, 2009). Also, their high densities reported in Andean rivers (JACOBSEN and MARÍN, 2007; JACOBSEN, 2008) indicates that they may represent a key agent in the functional ecology of these rivers, but its role is not well known. For example, HARGRAVE (1970) reported that although *H. azteca* can be omnivorous, it feeds mainly on algae and bacteria associated with sediment and macrophytes. Meanwhile, CASSET *et al*. (2001) found that in the river Lujan (Argentina), two species of *Hyalella* shared the same habitat: while *H. curvispina* consumed the phytobenthos, the other species (not identified) was feeding on the former. However, CAPELLO *et al*. (2004) reported that in the Paraná River, *H. curvispina* lives as a scraper of periphyton and as a predator. Similarly, specialization in microhabitat and the resulting distribution of food resources allowed the coexistence of two sympatric species of *Hyalella* in Brazil: *H. pleocuta* and *H. castroi* (DUTRA *et al*., 2007, DA SILVA and BOND-BUCKUP, 2008).

In high Central Andes (between 15º S and 24 ºS, and from 3500 m altitude), the native riparian vegetation suffer constant pressure not only from deforestation, where tree coverage gradually is reduced and replaced by grasses and other herbaceous (GARCÍA and BECK, 2006) but also from the introduction of exotic species (*Eucalyptus globulus* and *Pinus* spp.). Several authors have shown that the introduction of exotic species can cause major changes in trophic processes, altering the quantity, quality and residence time of debris in rivers (CASAS and GESSNER, 1999; YEATES and BARMUTA, 1999) and consequently the benthic community structure and ecosystem functionality (LESTER *et al*., 1994; CANHOTO and GRAÇA, 1995).

Therefore, considering the importance of *Hyalella* in the composition of the benthic community in Andean rivers (JACOBSEN, 2008) and the abundance of exotic plant species on the banks of the Andes, our objectives were (i) to determine the food habits of *Hyalella* sp. in the upper basin of the Cañete River and (ii) to assess *in situ* the feeding activity of *Hyalella* sp. on two types of leaves: *Polylepis* sp. a native plant species and *Eucalyptus globulus*, an introduced plant species.

2. Methods

2.1. Study Area

This study was conducted in the upper basin of the Cañete River (province of Lima) on the central coast of Peru. The sampling point, located at 3817 m a.s.l. (12º 06' 45''S, 75º 49' 00''W) corresponded to a third-order river located 500 meters downstream from the mouth of the lagoon Papacocha. The weather data available for the study area is limited: only rainfall data are available from the National Office for the Assessment of Natural

Resources of Peru (ONERN, 1970), and the baseline of the Platanal Hydroelectric Project (WALSH, 1999) covering the period between 1964 and 1984 at the meteorological station of Vilca (3 km downstream from the sampling point). During this period the rainfall was markedly seasonal, with recorded extreme monthly averages of 1.6 and 186.2 mm during the months of July and February, respectively, with an average annual total of 824.8 mm. The temperature varies considerably, from 7ºC at night to 20ºC during the day, with an annual average of 14ºC.

This sector of the basin is characterized by heavy deposition of calcium carbonate in the form of travertine, which is caused by high calcium concentrations in the water and the presence of groundwater spring upstream of the sampling point (ACOSTA, 2009). In, the study area, the riparian vegetation was represented by a complex tree structure dominated by the native species *Escallonia resinosa* which generated a complex river habitat with leaves and fallen branches in the water. This area is one of the few relatively intact riparian areas along the Cañete River.

In between the riparian area, and depending of the light penetration, dense populations of bryophytes, submerged macrophytes (*Myriophylum* sp., *Potamogeton* sp.), and submerged riparian vegetation (*Senecio* sp.) developed on the river channel, that is covered by the deposition of travertine. Further details of the chemistry of this ecosystem are available in ACOSTA (2009). The physicochemical characteristics of the water in the sampling area are presented in Table 1.

2.2. Gut content analysis of Hyalella sp.

To determine the food of *Hyalella* sp. we examined the gut contents of 10 individuals collected from each of the following habitats: two dominated by macrophytes (*Potamogeton* sp. and *Myriophyllum sp.*), one dominated by bryophytes, one with leaf litter of *E. resinosa*, and one with only travertine deposits.

Using forceps and fine knifes we dissected each individual and removed the digestive tube. Then, we prepared two slides for each habitat, each with five gut contents. All guts were completely full, so there was no difference in the percentage occupancy between individuals. Each gut was opened and spread on a drop of glycerin, and a coverslip was placed on top of it. The gut content analysis was performed by estimating the percentage composition of five predetermined categories of substrates: coarse particulate organic matter (CPOM: >1mm), fine particulate organic matter (FPOM: <1 mm), algae, chitin and minerals. The visual fields were analyzed under a microscope at a magnification of 100X.

This data did not present a normal distribution and were therefore analyzed using a Friedman's ANOVA to test significant differences (P < 0,05; and P < 0,001)in the diet of *Hyalella sp.* collected in each habitat. Then, pairwise Mann-Whitney U-tests were used to detect significant differences between two habitat types.

2.3. Feeding activity of Hyalella sp. with two types of leaf litter

Ten mesh bags were prepared (10 x 8 cm) each with 250 µm mesh, five of them containing freshly fallen *E. globulus* leaves of similar size, and the other five containing leaves of *Polylepis* sp., both from areas relatively close to the place of study. The bags were then left submerged for a conditioning period of 14 days in the riverbed. Subsequently, the water was drained off and the leaves were left at ambient temperature. We built 30 chambers, which consisted of plastic cylinders 10 cm long and 4 cm wide. Both ends were sealed with 250 µm mesh. Within each chamber 20 individuals of *Hyalella* sp. were placed in their last stage of development. Then, five leaves of *Polylepis* sp. were added to ten of the feeding chambers, and two leaves of *E. globules* to the other 10 feeding chambers. Additionally, we prepared control chambers, to assess weight loss of the leaves without the intervention of the amphipod: 5 chambers for each one of the leaves species.

The chambers were placed in rapids on the stream for three days and tied with rope to the shore vegetation to prevent their being swept away. After that time, for each chambers the individuals of *Hyalella* sp. were counted and the dry weight of leaves was determined in the laboratory where they were dried for 3 days at 60ºC. Although it was not possible to obtain initial weights of the leaves, we extrapolate the initial weight; from identical samples of each leave species which were dried and weighted.

Food consumption was expressed in terms of mg of weight loss during the experiment (three days). Mann-Whitney non-parametric test was used to test for differences between leaf litter consumption of both species.

3. Results

3.1. Gut content analysis of Hyalella sp.

The composition of gut content of *Hyalella* sp. is shown in Figure 1. The main component of the diet of *Hyalella* sp. was FPOM in most habitats: travertine had the highest proportion (69.5%), while in *Myriophyllum* and bryophytes the proportion was similar (58.5% and 56.8%, respectively). The only habitat in which CPOM made an important contribution was *E. resinosa* (68%). The remaining proportion of the gut content (approximately 40%) in most habitats was mineral particles, from the precipitated calcium carbonate. Traces of chitin, which indicates a predatory behavior, were present in almost all of the subjects tested (except those from the travertine habitat)

Friedman's ANOVA (Table 2) showed significant differences ($P < 0.001$) in the diet composition of *Hyalella* sp. in each habitat. The differences between the three main components in the gut content (FPOM, CPOM and Mineral) were analyzed with the Mann-Whitney U-test ($P < 0.05$) (Table 3), which showed that the statistically significant differences in CPOM and FPOM were in the individuals collected in *E. resinosa* leaf litter in relation to other habitats.

3.2. Feeding activity of Hyalella sp. using two types of leaf litter

The weight loss of *Polylepis* sp. was significantly greater than that of *E. globulus* (Table 4, Fig.2) both in the control and in the experimental chambers. Although the number of replicates was the same for the two species of leaves, 3 of the experimental chambers were swept away. The twenty individuals of *Hyalella* sp. consumed in three days a significantly greater amount of leaf litter of *Polylepis* sp., (0.025 mg/day) than *E. globulus* (0.008 mg/day). (Mann-Whitney, P = 0.00008). Also the natural decay was significantly higher in *Polylepis* sp. than in *E. globulus* (Mann-Whitney, P = 0.016).

4. Discussion

Although in temperate rivers amphipods traditionally have been considered to be shredders of leaf litter (CUMMINS and KLUG, 1979; TACHET, 2000) recently other studies have shown some degree of trophic plasticity in both genus, *Gammarus* (KELLY *et al*., 2002; FELTEN *et al*., 2008) and *Hyalella* (CASSET *et al*., 2001; CAPELLO *et al*., 2004; WANTZEN & WAGNER, 2006).Based on gut content analysis of *Hyalella* sp. in headwaters of the Cañete River, our data suggest an evident flexibility in its diet, consuming a broad variety of benthic food items as CPOM, FPOM, chitin and algae. This is consistent with others studies in South America; e.g. CAPELLO *et al*. (2004), who found that in the Parana River, *H. curvispina* behaved as predator and scraper of epiphytic algae. Also, CASSET *et al*. (2001) reported two species of *Hyalella* in the Lujan River (Argentina) each with different diets, based on consume of algae and other macroinvertebrates. In this way, our study reinforces the hypothesis that in tropical rivers, macroinvertebrates tend to be more omnivorous than in temperate rivers (COVICH, 1988; TOMANOVA *et al*., 2006).

Our analysis has shown that this trophic plasticity in the diet of *Hyalella* sp. may be observed in different habitats sampled in the river. So, whereas in bryophytes patches or in travertine layers, the diet of *Hyalella* sp. consisted by FPOM and its trophic role was mainly collector-gatherer; in leaf litter of *E. resinosa*, changed to be almost exclusively a shredder of CPOM. This variability in diet of *Hyalella sp*. is determined by the different supply of trophic resources in each habitat and is conditioned by factors such as composition of riparian vegetation (LI and DUDGEON, 2008) and variability of discharge (PEARSON *et al*., 1989).

In headwaters of the Cañete river, is often that riparian areas are dominated by grassland, which represent a continuous and elevated inputs of FPOM, but scarce of CPOM. In contrast, the scarce patches of native forests found in the riparian zone represent a significant source of leaf litter (and CPOM). Similar results found RÍOS *et al.* (2009) in a Andean stream in Ecuador, where the diet of *Hyalella* was composed mainly by CPOM (by gut content analysis), which originated from large amounts of allochthonous material exported from a dense riparian vegetation. On the other hand, in our study, the scarce representation of algae in the composition of diet of *Hyalella* sp. may be influenced by the used methods to recognize the food items. HARGRAVE (1970) by using stable isotope analysis found that algae are a significance component in the diet of *Hyalella azteca*, but that a large proportion of them are assimilated very quickly and its importance can be underestimated in standard microscopic methods. More recently, MANTEL *et al*. (2004) and LI and DUDGEON (2008) suggested that autochthonous energy sources may have a particularly important role even in shaded tropical streams. In our study area, the importance of algae in diet of *Hyaella* sp may be more important than we find. Further studies in tropical streams are needed to investigate this hypothesis for *Hyalella* sp.

Dominance of *Hyalella* in virtually all habitats of headwaters of the Cañete River, with very high densities ($7x10^4$ indiv./m^2) in areas cover with mosses (Acosta, 2009) suggests a successful adaptation to the gradient of environmental conditions in the bed river. Trophic flexibility in exploiting various types of food resources should represent an important advantage in the colonization of different habitats. We suggest that in this area of study, *Hyalella* sp. behaves as an opportunistic omnivore, feeding on different types of food substrates, preferably FPOM and CPOM.

Likewise, our results with the experiments *in situ* showed that although *Hyalella* sp. was able to consume exotic leaf litter (*E. globulus*) moreover, their consumption rate is lower compared to the native plant (*Polylepis* sp.). These results are according to others previous results obtained in *E. globulus* that emphasized the low nutrient concentrations (POZO *et al.*, 1998; SAMPAIO *et al.*, 2001) and the presence of secondary compounds like tannins, lignin and cellulose that inhibit the processing of leaf litter and growth of macroinvertebrates (WEBSTER and BENFIELD, 1986; BENSTEAD, 1996; GRAÇA, 2001; SAMPAIO *et al.*, 2001). As mentioned by YEATES and BARMUTA (1999) and GRAÇA *et al*. (2001), more important than the geographical origin of organic matter that enters the river is its chemical composition and the intrinsic characteristics of the leaves which may or not facilitate their consumption. More recently, GRAÇA and CRASSA (2010) suggested that leaf toughness can be an important factor in the paucity of shredders in tropical streams. In this sense, *Hyalella* sp. shows the same feeding tactics that their counterparts of temperate regions. Likewise, the smaller body size (and therefore their mouthparts) of the species of *Hyalella* present in the river Cañete, compared to *Gammarus* in temperate rivers, can also be a important disadvantage in the processing of leaf litter of high hardness as *E. globulus*, such as has been suggested in other studies (WANTZEN and WAGNER, 2006). Accordingly with FELTEN *et al*. (2008) we propose that, microhabitat type as much as body size may be highly significant factors that influence diet of amphipods.

Tropical deforestation of native forests and the increasing introduction of exotic species such as *E. globulus* represent important changes in the composition of the riparian vegetation of Andean rivers. Consequently, this allochthonous material exported to river ecosystem can directly affect the natural processing of organic matter, because *E. globulus* leaves have mentioned to as being of poor quality and slow breakdown rate (BOULTON, 1991; GRAÇA *et al*., 2002). Therefore, the low consumption rates of *E. globulus* found indicate that *Hyalella* sp., a potential shredder of allochthonous detritus in Andean rivers, not represent an important processor of this type of material.

In conclusion, the ubiquity of *Hyalella* sp. in the travertine system of the headwaters of the Cañete River and the plasticity of its diet shown in our results based on gut content analysis, indicate that this species behaves as an opportunistic omnivore, consuming the alimentary substrate that each habitat provides, both fine particulate organic matter (FPOM) and coarse (CPOM), in addition to other macroinvertebrates, mineral products of the deposition of travertine, and possibly algae. Also, during *in situ* experiments the species showed a major weight loss for leaf litter from the native species *Polylepis* sp. that the exotic species *E. globulus*.

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Table 1. Mean values of the physico-chemical water parameters measured in the headwaters of Cañete River, Peru (*n* = 22)

Parameters	Mean
Temperature (ºC)	12.09
Oxygen (%Sat)	69.88
pH	6.15
Conductivity (µS/cm^{-1})	445.11
Alkalinity (mg/l)	199.94
Ca^{+2} (mg/l)	101.81
Mg^{+2} (mg/l)	11.34

Table 2. Summary of Friedman's ANOVA to test significant differences in the diet of *Hyalella* sp.-(four food categories) collected in each habitat. (** = $P < 0.001$)

	X^2	df	p	Significance
Potamogeton	19,58	4	<0,001	**
E.resinosa	23,52	4	<0,001	**
Bryophytes	25,38	4	<0,001	**
Myriophylum	34,56	4	<0,001	**
Travertine	27,05	4	<0,001	**

Table 3. Summary of Mann-Whitney U-tests for the food categories included in diet of *Hyalella* sp. between pairs of habitats ($P < 0.05$).

	CPOM			**FPOM**			**Mineral**		
	U	**Z**	**p-level**	**U**	**Z**	**p-level**	**U**	**Z**	**p-level**
E. resinosa /Bryophytes	18.500	2.385	**0.017***	10.000	-3.126	**0.002***	47.000	-0.229	0.819
E. resinosa /*Myriophyllum*	3.000	3.674	**0.000***	0.500	-3.837	**0.000***	20.000	-2.288	**0.022***
E. resinosa /Travertine	6.000	3.401	**0.001***	6.500	-3.406	**0.001***	39.500	-0.801	0.423
E. resinosa /*Potamogeton*	19.500	-2.314	**0.021***	20.000	2.426	**0.015***	27.500	1.718	0.086
Bryophytes /*Myriophylum*	16.000	2.696	**0.007***	50.000	0.000	1.000	6.500	-3.344	**0.001***
Bryophytes /Travertine	20.500	2.308	**0.021***	37.000	-0.988	0.323	34.500	-1.192	0.233
Bryophytes /*Potamogeton*	47.500	-0.190	0.849	36.000	-1.064	0.287	22.000	2.154	**0.031***
Potamogeton /*Myriophyllum*	23.500	2.194	**0.028***	32.500	-1.346	0.178	43.000	-0.543	0.587
Potamogeton /Travertine	27.500	1.817	0.069	19.500	-2.331	**0.020***	38.000	0.923	0.356
Myriophylum /Travertine	45.000	-0.497	0.619	27.000	-1.766	0.077	28.000	1.697	0.090

Table 4. Statistical descriptors of weight loss (mg/day) of *Polylepis* sp. and *E. globulus* with (treatment) and without (control) *Hyalella* sp. in a feeding chambers *in situ* in headwater Cañete river.

	Valid N	Mean	Min.	Max.	Std. Dev.
Polylepis	5	0,011	0,002	0,022	0,083
	12	0,025	0,018	0,034	0,005
E. globulus	5	0,001	0,000	0,002	0,001
	15	0,008	0,003	0,028	0,007

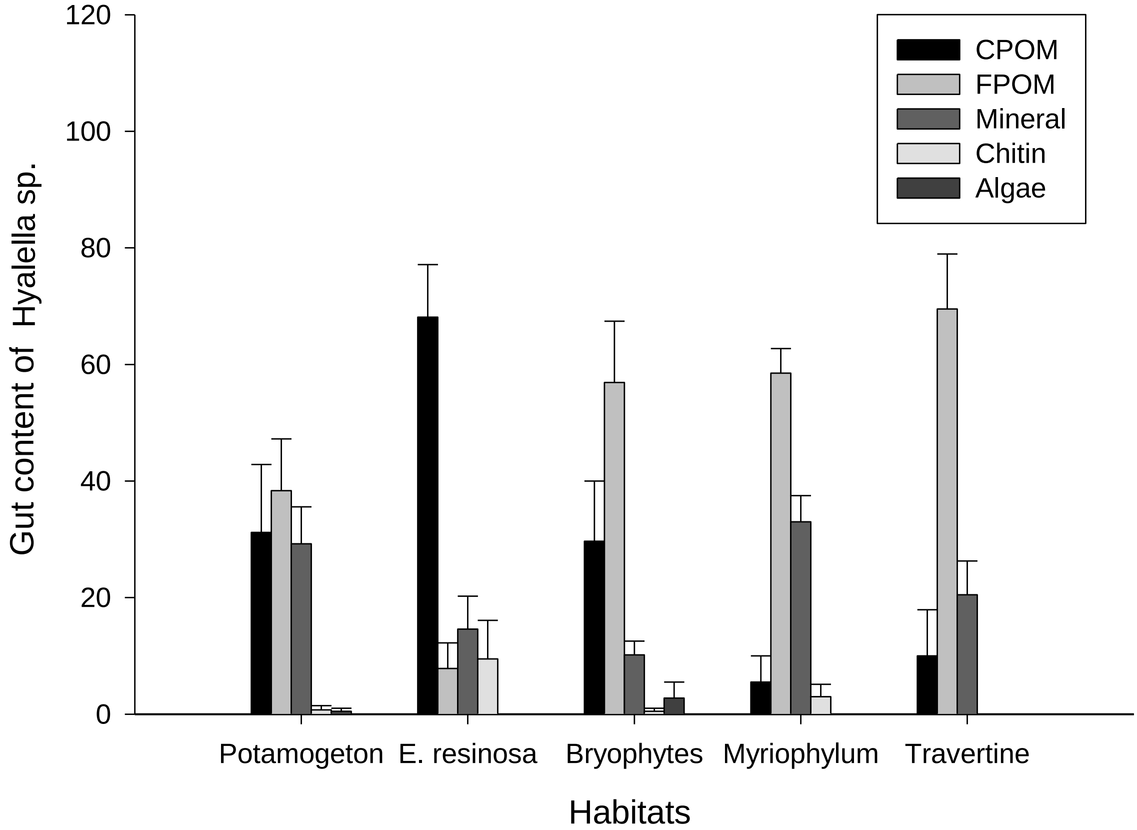

Fig. 1. Percent composition of the food categories in the gut content (mean ± *SE*) of *Hyalella* sp. in different habitats at Cañete River (Peru).

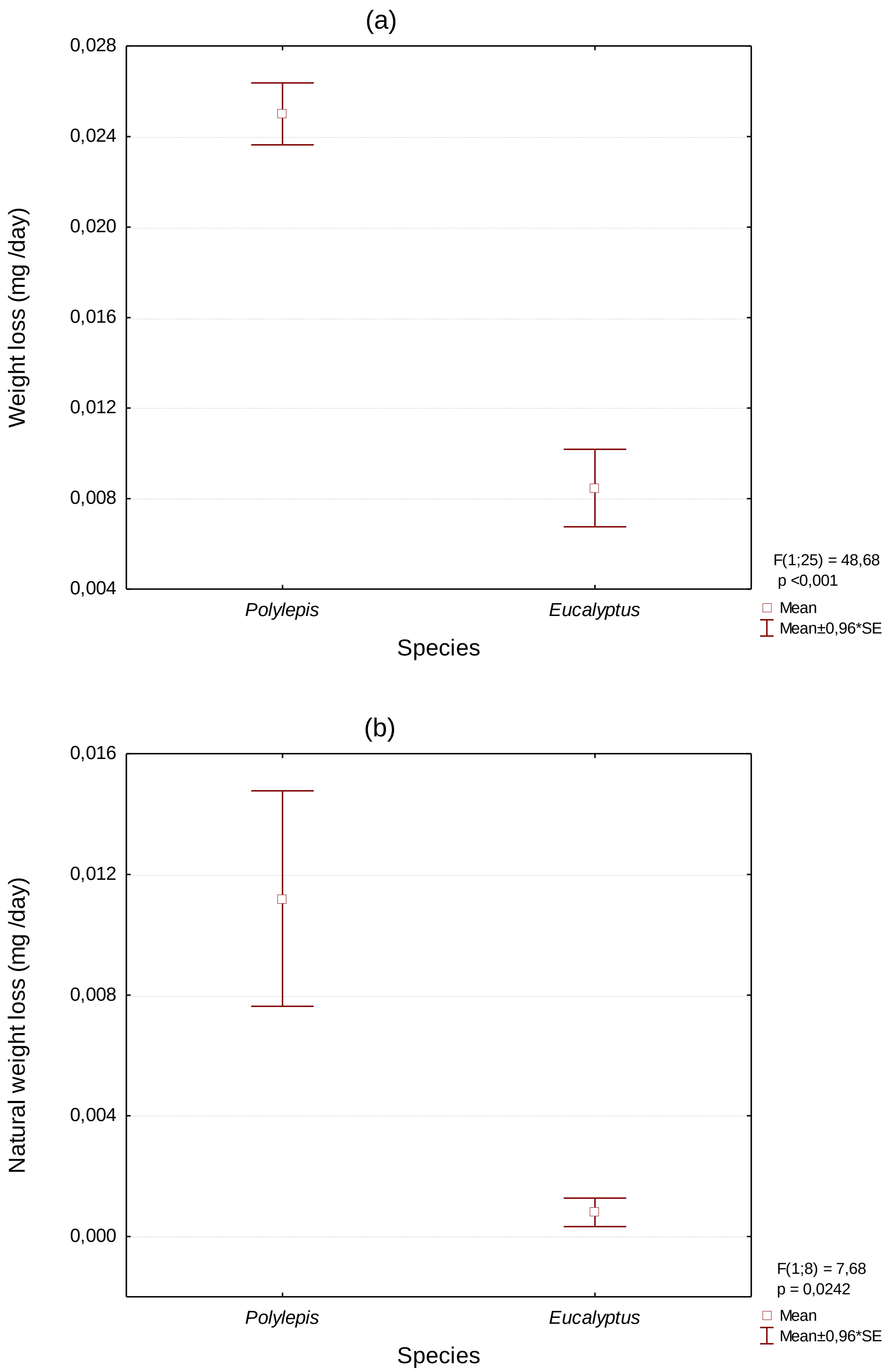

Fig. 2. Weight loss (mg/day) (mean ± *SE*) of *Polylepis* sp. and *E. globulus* with. (a) and without *Hyalella* sp.(b).