

Feeding plasticity and growth of two Plecopteran larvae in a low order Andean stream

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Introduction

The study of feeding habit and assimilation efficiency of aquatic invertebrates contributes to understand stream processes by linking basic food resource categories to higher trophic levels (Mihuc, 1997). This functional approach involves two ecological aspects: one is associated with food intake, and the other one concerns with matter and energy transference through food webs. Morpho-behavioral adaptations for obtaining food of invertebrates (i.e. the food acquisition systems) are expected to be less selective than the biochemically-based assimilation system (Cummins and Merritt, 1996). We understand feeding plasticity of an organism as its capability of displaying a wide range of food acquisition among available resources. Available food for invertebrates is just a fraction of the potential food resource present in a system to which organisms can access. True availability means that no interference is involved that automatically excludes some of the items, e.g. morphological-behavioral specialization of the species (Cummins, 1973). Although feeding plasticity is more common than previously thought among lotic invertebrates (Friberg and Jacobsen, 1999) not all food ingested is likely to be transformed into body tissue. Growth measurements or efficiency of food conversion estimates indicate to what extent organisms match with contrasting food resource categories. Species that show significant body growth (Mihuc and Minshall, 1995) or significant assimilation efficiency (Cummins and Merritt, 1996) when fed on more than one kind of food are considered as generalists.

Functional feeding classification of aquatic organisms enhances the knowledge of trophic dynamics in streams because they simplify the benthic community into trophic guilds, interpreting the trophic stream dynamics based on functional group responses (the functional feeding group approach; Cummins, 1996). The extensive study of Palmer and O'Keeffe (1992) and Palmer *et al.*, (1993a, b) concluded that feeding behavior, gut content and mouthpart morphology analyses provided the most certain FFG (functional feeding group) designations in 12 taxa of insects from a South African river. On the other hand, Mihuc and Mihuc (1995) stressed that food habits do not necessarily reflect an accurate assessment of functional trophic relationships for benthic invertebrates since most taxa may function as generalists even when reported as specialists. The

Abstract

Feeding plasticity and growth efficiency of the plecoptera *Klapopteryx kuscheli* and *Notoperla archiplatae* were tested on leaf litter and periphyton through *in situ* experiments. *N. archiplatae* showed the highest consumption and growth rates when fed on periphyton but it failed to feed on leaf litter. *K. kuscheli* was able to feed on periphyton, though it did not grow. Therefore, only *K. kuscheli* showed feeding plasticity on the contrasting resources offered. Nevertheless both plecopteran species are highly specialised only on the food resource that they commonly exploit in nature.

Keywords: trophic ecology, consumption, assimilation efficiency.

food habit of the Andean plecoptera *Klapopteryx kuscheli* (ILLIES, 1960) and *Notoperla archiplatae* (ILLIES, 1958) had been previously assessed following Palmer *et al.* (1993a, b) (Díaz Villanueva and Albariño, 1999; Albariño, 2001). Mouthpart morphology of these species were fitted into the Type I (detritivore-herbivore) *sensu* Stewart and Stark (1988). They slightly differ in that the galea of *N. archiplatae* bears a dense brush of short and stout bristles, which is not present in *K. kuscheli*. Both taxa displayed contrasting trophic habits in nature. *K. kuscheli* showed to be a detritivore-shredder while *N. archiplatae* behaved as a periphyton brusherscraper.

The main goal of this study was to test to what extent two important aquatic invertebrates of low order Andean streams were capable of exploiting different food resources and converting it to secondary production. We examined *in situ* feeding and growth rates, survivorship and efficiency of conversion of ingested food using two major food items: periphyton and leaf litter. We selected these two food resources because they are the most representatives in fast flowing habitats where these plecopterans live: periphyton being more abundant on exposed stone surfaces and leaves being retained between and below stones. We also aimed to test if the FFG classification of a taxon is possible on the combined analysis of mouthpart morphology, gut content and feeding preference experiments. We experimentally tested this contention by verifying whether such taxa previously assigned to one guild were able to act in a different functional feeding group, thus displaying a generalist strategy.

Material and Methods

Study area

The experiment was conducted in a nameless tributary of Ñireco stream (Fig. 1). This stream runs into Nahuel Huapi lake (Argentina) and the tributary is located in the upper section of its catchment (41° 13' S; 71° 20' W). The basin drains a *Nothofagus pumilio* (POEP. & ENDL.) KRASSER forest. In Patagonian Andes, this deciduous beech constitutes the highest mountain belt of the temperate forest, up to the timberline (Hildebrand-Vogel *et al.*, 1990). The basin has a pluvio-nival hydrological regime with high discharge periods in fall (rain) and spring (snowmelt) and low ones in late summer.

The tributary stream covers 2.9 km², and runs from 1900 m a.s.l. to its outlet into Ñireco stream at 1065 m a.s.l. The overall slope of the streambed is 30%. Conductivity is 49 µS cm⁻¹, pH is neutral to slightly basic (7.7) and dissolved oxygen concentration is always at saturation levels. The experiment was conducted in riffle areas where the bottom was dominated by boulders and cobbles and stream width was about 1-3 m.

Experimental design

Macroinvertebrates were collected in a stream reach below the experimentation site by picking up stones and dislodging them from the underside. All larvae were measured in the field under a stereomicroscope with a micrometer eyepiece to estimate initial body mass. Total body length and head width were measured at nearest 0.05 and 0.02 mm, respectively.

The experiment consisted in offering two single food resources to both plecopteran larval species in order to measure their capability of feeding just on a single food resource and also their ability to survive and grow under these extreme conditions. Two food treatments were performed: 1) periphyton and 2) leaf litter. Experimental units in periphyton treatment consisted of an 8 x 8 cm unglazed ceramic tiles, which served as biofilm substrate and to study the grazing activity of chosen species. Each tile was enclosed in a transparent plastic tube (10 cm length and 8 cm in diameter). The experimental chambers of the leaf litter treatment consisted of plastic tubes of the same size, but opaque (to avoid natural biofilm development) supplied with leaf litter. Chambers were closed at their tops with 1 mm mesh size net tied with elastic bands.

In each leaf litter chamber, we introduced 203 mg dry mass of non-pre-dried senescent undamaged *Nothofagus pumilio* leaves that were pre-hydrated to permit handling without damaging. They were held by petioles with a plastic strand and fixed at the centre of the chamber to avoid flow obstruction inside. Leaves were collected from the forest soil at abscission time, in the stream surroundings. In the laboratory, a leaf litter fresh mass (FM) – dry mass (DM) regression was established to estimate initial dry mass of leaf packs. Fresh and dry masses of leaves were obtained by drying material at 40°C for 24 hs or at 105°C for 48 hs, respectively.

Each feeding chamber was replicated 10 times for each plecopteran species. Controls for periphyton growth and leaf litter decay were run without larvae (n=6). In addition, opaque

chambers without food addition served as larval growth control (n=6).

All experimental units were introduced in the stream on March 3rd. All the units were randomly attached to 3 metal frames placed in a 40 m reach. Chambers were left 25 days prior the inclusion of macroinvertebrates for periphyton colonisation and leaf litter conditioning. On March 28th larvae were introduced one in each chamber. Simultaneously, 6 experimental units of each treatment were removed as initial controls. They were taken to the laboratory in individual plastic containers, thermally isolated and in total darkness. During the experiment, periphyton, sediments and fine particulate organic matter accumulation at the screens on top were removed at least once a week with a nylon brush to avoid clogging. After 44 days of experimentation, all the experimental units were taken to the laboratory to measure changes in periphyton, leaf mass and larval size.

Laboratory methods

Final body length and head width of each larva were measured to estimate final body mass. For each larval species, we obtained a regression for body ash free dry mass (AFDM) against body size from a set of larvae collected previously. Larvae were dried at 80°C for 24 hrs to obtain their dry mass and then combusted at 550°C during 1 hour for AFDM. The power equations that best fitted our data were:

$BAFDM = -0.84 + 2.83 POW^{1.92}$ (for *K. kuscheli*; $r^2_{adj}=0.84$; s.e.=4.46, n=110), and

$BAFDM = 1.54 + 0.03 BL^{2.35}$ (for *N. archiplatae*; $r^2_{adj}=0.79$; s.e.=4.39, n=68), where BAFDM, POW and BL were body ash free dry mass (mg), post-ocular width (mm) and body length (cerci excluded) (mm), respectively. Larval growth was calculated as the difference between initial and final biomass.

Periphyton was scrapped from each tile with a razor blade and washed with distilled water. Periphyton biomass was determined in terms of AFDM and expressed per square centimetre. Each sample was filtered onto pre-weighed Whatman GF/C filter and dried at 80°C for 1.5 hours. The filters were weighed and incinerated (APHA, 1989). The remaining leaf material was examined by naked eye in search of shredding signs. Leaf matter was then dried at 105°C for 48 hs to obtain dry mass and then incinerated to obtain its ash free dry mass.

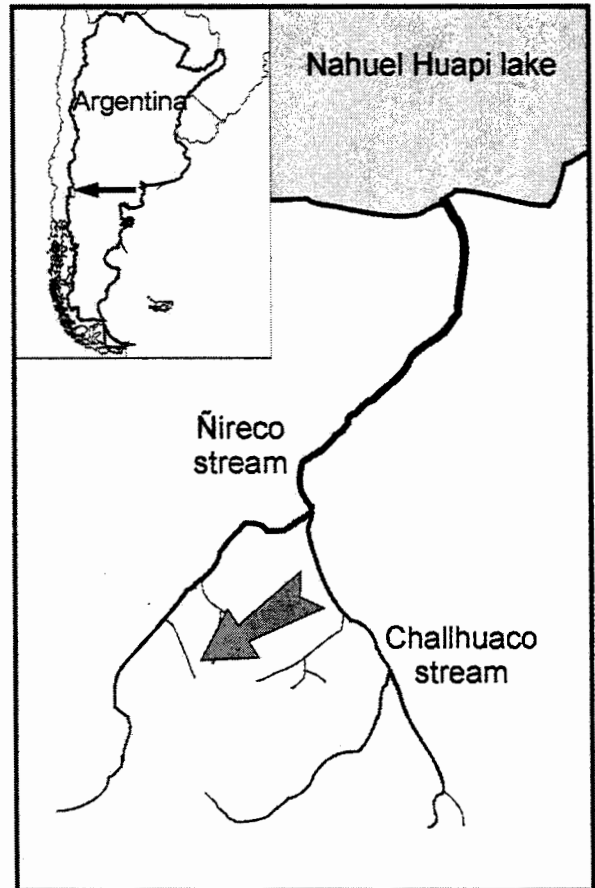


Fig.1 - Geographic location of the nameless tributary of Ñireco stream where the study was run.

Larval instantaneous rates for both consumption and growth were referred to initial body mass for comparison purposes. Thus, relative consumption rate (RCR) and relative growth rate (RGR) were expressed in percentage per day (% d⁻¹). Net values were obtained by subtracting mean controls to each experimental replicate. Efficiency of ingested food was defined as the ratio between net food intake and net body growth expressed in percentage (ECI%) (Arsuffi and Suberkropp, 1986):

$$ECI = \frac{FBc - FBt}{IBt - IBs} \times 100$$

where FBc is food biomass in controls and FBt in treatments, IBt is the insect's biomass in treatments and IBs is the starved insect's biomass.

Data were tested for significant differences by using one or two-way ANOVA. Multiple comparisons were tested with *a posteriori* methods (Student-Neuman-Keuls; S-N-K). Significant differences were tested with 95% of confidence.

Results

After 44 days of experimentation, more than 50% of larvae were still alive in treatments and control. The highest larval survivorship was observed for *N. archiplatae* fed on periphyton (90%). However, in control chambers (with no food addition) 66% of *N. archiplatae* larvae survived while those of *K. kuscheli* presented a survivorship of 80%, indicating that the former was more susceptible to starving conditions. In leaf litter chambers, *N. archiplatae* survived at almost the same percentage as it did in control (60%). In contrast, *K. kuscheli* showed the same survivorship on both food items and in control chambers (80%).

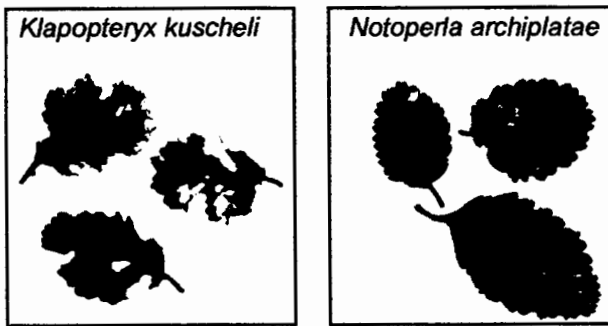


Fig. 2 - Photographs of consumed *Notophagus pumilio* leaves from *Klapopteryx kuscheli* and *Notoperla archiplatae* chambers showing signs of feeding activity. Leaves were abundantly shredded by *K. kuscheli*, but scarcely abraded by *N. archiplatae*.

Visual observation of leaves from *K. kuscheli* chambers showed abundant shredding signs while they were absent in control leaves. On the other hand, feeding activity of *N. archiplatae* was scarcely found. These larvae did not bite but slightly abraded leaves (Fig. 2). This effect was probably the result of a persistent browsing activity that *N. archiplatae* carried out using the brush of galeae and the scoop-like laciniae described by Díaz Villanueva and Albariño (1999). However, this activity was not enough to cause a significant reduction of leaf mass, thus its relative consumption rate was null (ANOVA, $P < 0.05$) (Fig. 3). Leaves ingested by *K. kuscheli*

represented 4.8% of its initial body mass *per day* (Fig. 3). On the other hand, *N. archiplatae* showed a daily consumption rate of 10.0% of its initial body mass and they consumed 62% more periphyton than *K. kuscheli* (S-N-K's test, $P < 0.05$) (Fig. 3). Algal consumption by *K. kuscheli* on periphyton treatment was confirmed by the observation of gut contents, which showed the presence of diatoms (especially the filamentous *Melosira varians*). Therefore the laciniae with apical pointed teeth and concave inner margin (Albariño, 2001) might have been used to feed also on algae as confirmed by the corresponding high consumption rates.

As regards larval growth, it was significant only for *N. archiplatae* feeding on periphyton and for *K. kuscheli* on leaf litter (S-N-K's test, $P < 0.05$) (Fig. 4). The relative growth rate on leaves was 6.5 times higher for *K. kuscheli* than for *N. archiplatae* ($P < 0.05$) (Fig. 4). On the other hand, the RGR on periphyton for *N. archiplatae* was significantly higher than for *K. kuscheli* which yielded a negative value ($P < 0.05$) (Fig. 4). The efficiency of food conversion into body biomass (ECI) was calculated only for *K. kuscheli* fed on leaf litter and for *N. archiplatae* on periphyton because the other conditions achieved negative values of consumption and/or growth. *K. kuscheli* converted 14% of the consumed CPOM (coarse particulate organic matter) into body mass while the ECI for *N. archiplatae* on periphyton was 5% (Fig. 5).

Discussion

In this study we tested to what extent two important aquatic invertebrates in low order mountain streams were capable to exploit other resource than the one they do in nature and if they can grow using such resource. Our results demonstrated that *K. kuscheli* was able to make use of both food resources while *N. archiplatae* was not. Moreover, larval growth in both species was only achieved when they fed on the resources they use in nature.

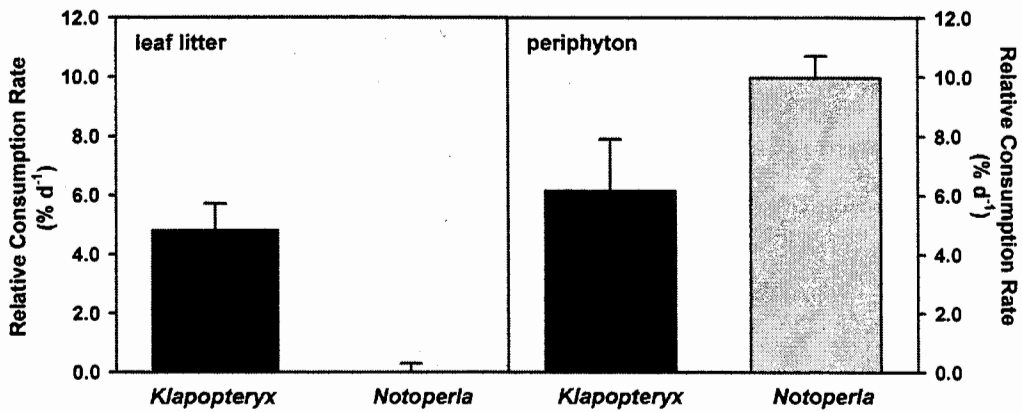


Fig. 3 - Relative consumption rate of *Klapopteryx kuscheli* and *Notoperla archiplatae*, expressed as percentage of AFDM consumed food (leaf litter and periphyton) by initial individual larval AFDM per day. Error bars represent standard error.

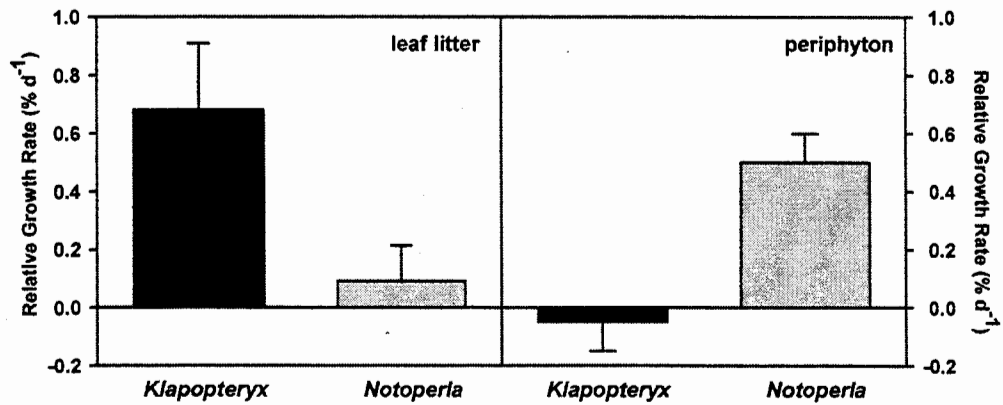


Fig. 4 - Relative growth rate of *Klapopteryx kuscheli* and *Notoperla archiplatae*, expressed as percentage of body AFDM gained by initial individual larval AFDM per day. Error bars represent standard error.

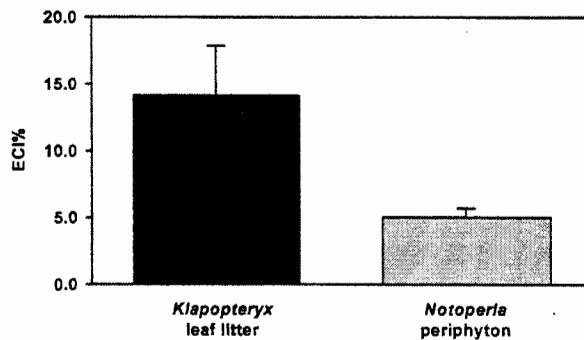


Fig. 5 - Efficiency of conversion of ingested food (ECI) of *Klapopteryx kuscheli* fed on leaf litter and *Notoperla archiplatae* fed on periphyton. Error bars represent standard error. Values for *N. archiplatae* fed on leaf litter and *K. kuscheli* fed on periphyton were not calculated because consumption and growth failed respectively.

K. kuscheli consumed leaves and periphyton at the same rate (Fig. 3) showing it could display similar ingestion efficiency on such dissimilar resources. In this sense, Friberg and Jacobsen (1994) found that two shredders, the trichopteran *Sericostoma personatum* and the amphipod *Gammarus pulex*, had almost the same consumption rate for two contrasting food types (the filamentous alga *Microspora* and leaf litter). They stressed that feeding plasticity in the detritivore-shredder guild may be more common than traditionally reported. In our experiment, *K. kuscheli* was very efficient in feeding on CPOM, but it was not the same for *N. archiplatae*. When there is no food-choice, feeding should occur on the single offered item, unless it was not available. *N. archiplatae* was not able to feed on leaf material indicating a lack of feeding plasticity. Although other grazers can feed and even grow on leaf litter using their brushing-adapted or scraping-adapted mouthparts (Mihuc and Minshall, 1995; Cummins and Merritt, 1996), it was neglectable in *N. archiplatae*. Our results suggest a mismatch of its morpho-behavioral adaptations to exploit this resource, e.g. bristles on the tip of the lacinia cannot be used in strong shredding (Arens, 1990).

Despite his high consumption rate, *K. kuscheli* failed to grow on periphyton, which indicated that assimilation efficiency was low for this item or that energy gained by food assimilation was allocated to handling and ingestion. The efficiency with which ingested food is converted to growth (ECI) is dependent on the digestive capabilities (i.e., assimilation system). In general, aquatic insects would be expected to ingest foods that are most efficiently assimilated (Cummins and Merritt, 1996). This contention agrees with the results of the present study and the diet reported for both plecopteran in the stream (Díaz Villanueva and Albariño, 1999; Albariño, 2001). However, when food quality is low, larval consumption should increase to balance the benefit/cost equilibrium for its decreased nutritional value (Cummins and Klug, 1979). *K. kuscheli* in the periphyton treatment tried to compensate for such a non-profitable food by ingesting it at almost the same rate as on leaves and it allowed, at least, to maintain its survivorship.

Little empirical information exists about how the assimilation of resources varies among lotic primary consumers, including those with generalist or specialist strategies (Mihuc, 1997). Many invertebrates are trophic generalists,

capable of using two or more resources for growth (Mihuc and Minshall, 1995; Friberg and Jacobsen, 1999). Our findings support that two representatives of the Southern Hemisphere related families (Austroperlidae and Gripopterygidae) are not generalists as they were not able to grow on contrasting food and their assimilation efficiencies were also negligible on such resources. Other Gripopterygidae that have more generalized mouthpart morphology (i.e. without specialized adaptations in galeae), are able to feed on a wide range of items [e.g. Australian Gripopterygidae (Sephton and Hynes, 1983) and other South American Gripopterygidae (Clever Polegatto, unpublished data)] and might also grow on contrasting resources. Facultative species would be expected to exhibit a wide range of food resource use but low efficiency, while obligate (specialist) taxa would exhibit the highest efficiency on the matching resource and very low efficiency on others (Cummins and Merritt, 1996).

The ECI of *K. kuscheli* on leaf detritus and *N. archiplatae* on periphyton were significantly positive. The efficiency of *K. kuscheli* (14%) was higher than the ECI calculated for the same species and food item (*N. pumilio* leaf litter) in a side-channel experiment [4% (Albariño and Balseiro, 1998)]. It is likely that differences between experimental designs had conducted to those dissimilar values. In the present experiment, handling procedures were lowered as much as possible and the study was run at the same stream where larvae inhabited. The efficiency with which *K. kuscheli* converted leaf litter in body mass is in the range of the ECI obtained for other shredders as the plecopteran *Pteronarcys scotti* [4% (McDiffett, 1970)], the trichopteran *Anabolia nervosa* [ECI range: 12-16% (Jacobsen and Sand-Jensen, 1994)] and *Sericostoma personatum* [ECI range: 2-15% (Friberg and Jacobsen, 1999)] on various leaf species. It was the first time that an ECI for *N. archiplatae* was calculated and it was done in its environment, as this species is very vulnerable to handling. In contrast with our expectation, this species feeding on periphyton showed a relative low efficiency (5%) with regards to other herbivores [e.g. 20% for the grazer *Baetis* sp. (Cummins and Klug, 1979)]. Grazing activity is known to produce algal removal (Lamberti *et al.*, 1987), so it is probable that periphyton consumption had been overestimated, and consequently the ECI for *N. archiplatae* had been underestimated.

The single inspection of mouthpart morphology or gut content analysis is not entirely

enough to infer food habits (Cummins and Merritt, 1996). A combination of those approaches with feeding experiments or feeding behavioral observation has demonstrated to be very suitable for an accurate assignation of invertebrates to their corresponding FFGs (McShaffrey and McCafferty, 1988; Palmer *et al.*, 1993a, b). In this study we confirmed the previously reported narrow feeding habit of *K. kuscheli* on coarse organic detritus and *N. archiplatae* on periphyton.

In terms of trophic ecology, herbivore-detritivore specialists are expected to outcompete generalists as the former achieve higher efficiency of food conversion (Cummins and Merritt, 1996). However, a generalist strategy would be best adapted during unpredictable changes in environmental conditions when particular resources are unavailable. Watershed alteration that impose changes in the input timing, standing crop or quality of basic primary resources could strongly affect the studied populations.

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