

DIET AND FUNCTIONAL FEEDING GROUPS OF CHIRONOMIDAE (DIPTERA) LARVAE IN ALPINE FRESHWATER HABITATS

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Abstract

A gut content analysis (GCA) was performed to quantify the relative use of food resources by larvae of chironomids (Diptera: Chironomidae) inhabiting different Alpine freshwater habitats fed by meltwater (kryal), groundwater (krenal) and mixed waters (glacio-rhithral, proglacial pond) in the Italian Alps (Trentino). GCA was performed on the 13 most frequent and abundant taxa in these habitats: *Diamesa bertrami*, *Diamesa latitarsis*, *Diamesa steinboecki*, *Diamesa zernyi*, *Pseudokiefferiella parva*, *Eukiefferiella minor*, *Metriocnemus eurynotus* gr., *Parametriocnemus stylatus*, *Thienemanniella clavicornis*, *Tvetenia calvescens*, *Macropelopia* sp., *Zavrelimyia* sp., *Micropsectra atrofasciata* gr. Guts were removed, mounted in Canada Balsam, and examined under a microscope (1000x). The gut of each individual was assumed to be 100% full, and proportions of the different food items were estimated using a 10x10 grid designed with the NIS-BR software. Food items were divided into 10 categories: Mineral Material, Animal Tissue, Algae (except diatoms), Diatoms, Plant tissue, Amorphous detritus, Lichens, Bryophytes, Fungi, and Pollen. The gut content of different taxa contained significantly different ($p < 0.05$) food categories based on a non-parametric statistical test. Differences in the diet were observed between species living in the same habitat type and classified into the same trophic category (detritivores, grazers, or predators) and individuals belonging to the same species living in different habitat types. A certain trophic flexibility and omnivory was found, which may facilitate the adaptation of chironomids to changes in available resources due to glacier retreat.

Introduction

Chironomids (Diptera: Chironomidae), commonly known as non-biting midges, are a highly diverse and ubiquitous family of dipteran insects. They in-

habit a vast array of aquatic and semi-aquatic environments worldwide ranging from oligotrophic mountain streams to eutrophic lowland lakes, temporary ponds, peat bogs, wet soil, and marine waters (Armitage et al. 1995) and are the sole insect taxon in specific habitats such as glacier-fed streams and springs (e.g., Lindegaard 1995, Plóciennik et al. 2016, Lencioni 2018).

The life cycle of most species involves an aquatic larval stage, which can last from weeks to years, followed by a brief pupal stage and an emergent adult. As primary consumers, larval chironomids play a major role in aquatic food webs, facilitating the transfer of energy from lower trophic levels (e.g., algae, detritus) to higher consumers such as fish, birds, and terrestrial invertebrates (Tokeshi 1995, Hågvar et al. 2016). Given their significant contribution to ecosystem functioning and their widespread distribution, understanding the dietary habits of chironomid larvae is crucial for elucidating nutrient cycling, energy flow, and the overall health of aquatic ecosystems, especially where they dominate the invertebrate community, such as alpine streams and springs (Lencioni et al. 2012, Rossaro et al. 2016). Resource partitioning among phylogenetically close species has been a fundamental concept in the development of modern ecology, serving as a primary structuring force for communities (Pulliam 2000, Butakka et al. 2016). Analysing the larval diet at the species level provides crucial information for assessing a species' ecological role in any given ecosystem. This may help us to understand the interactions between a species and its environment and between different species. Resulting information may lead to enhanced understanding of trophic community structures, ultimately providing better understanding of how these insects colonize specific habitats (Ingvason et al. 2004). Despite numerous studies carried out on Chironomidae, detailed investigations into the specific dietary components and

feeding behaviours of alpine chironomid species remain limited.

Previous studies have ascribed chironomid genera and species to different trophic groups (e.g. detritivores, predators, algivores, phytophages, xylophages, parasites, and commensals) and different feeding strategies (gatherers, suckers, filterers, shredders, scrapers) (e.g. Coffman and Ferrington, 1996, Tavares-Cromar and Williams, 1997, da Silva et al., 2008, Sanseverino and Nessimian, 2008, Galizzi et al., 2012, and Merritt et al., 2019). Moog and Hartmann (2017) merged trophic groups with trophic strategies, recognizing 10 main feeding types (recognized by the authors also as “functional feeding groups”) with associated specific food sources for chironomid larvae (Table 1): shredders, grazers, scrapers, rasps, active filter-feeders, eddy filterers, passive filter feeders, detritus feeders (gathering collectors), leaf borers, miners, piercers, xylophagous, predators, parasites, other feeding types/omnivorous. Armitage et al. (1995) recognized that most genera and species exhibit multiple feeding strategies and belong *de facto* to different trophic groups.

Additionally, what larvae eat may vary with the developmental stage, i.e. early instar larvae (I–II instars) could feed differently from mature larvae (III–IV instars) (Baker and McLachlan 1979, Olafsson 1992, Banegas and Rocha 2023). Sea-

sonality and food availability may also drive larval feeding strategies (algae, detritus and associated microorganisms, plant fragments, decomposing wood, fungi, pollen, and invertebrates) (Berg 1995, Henriques-Oliveira et al. 2003, Sanseverino and Nessimian 2008); furthermore, these factors are both influenced by environmental conditions and substrate type (Butakka et al., 2016). This makes the trophic categorization of chironomid species a challenging topic.

This study investigates the trophic ecology of chironomid larvae from various aquatic habitats in glacial catchments of the Alps. New insights are given on the ecological role of chironomids in streams and ponds with different glacial influence as well as on the degree of dietary specialization, and their capacity of using different food sources. The information gathered is expected to be highly valuable to foresee how glacial taxa will adjust their feeding habits in response to the habitat shifts and glacial recession currently underway due to global warming (Wilkes et al. 2023).

Materials and Methods

Study area and sampling sites

We analysed larvae collected in late summer 2022 from seven sites in four catchments (Fig. 1, Table 2), in three different mountainous groups in the Italian Alps (Trentino Province): Conca/Carè Alto

Table 1. Functional feeding groups (FFGs) according to Moog and Hartmann (2017). CPOM = Coarse Particulate Organic Matter -particles between 50 µm and 1 mm); FPOM = Fine Particulate Organic Matter – particles < 50 µm.

FFGs	Abbreviation	Sources of food
Shredders	SHR	Fallen leaves, plant tissue, CPOM
Grazers	GRA	Epilithic algal tissues, biofilm, partially POM
Scrapers, rasps		Endo and epilithic algal tissues, partially tissues of living plants
Active filter-feeders	AFIL	Food in water current is actively filtered
Eddy filterers		Suspended FPOM, micro prey is whirled
Passive filter feeders	PFIL	Food brought by flowing water current
Detritus feeders (gathering collectors)	DET	Sedimented FPOM
Leaf borers, miners	MIN	Leaves of aquatic plants
Piercers		Algae and cells of aquatic plants
Xylophagous	XYL	Woody debris
Predators	PRE	Prey
Parasites	PAR	Host
Other feeding types	OTH	Cannot be classified into this scheme
Omnivorous animals		Diverse

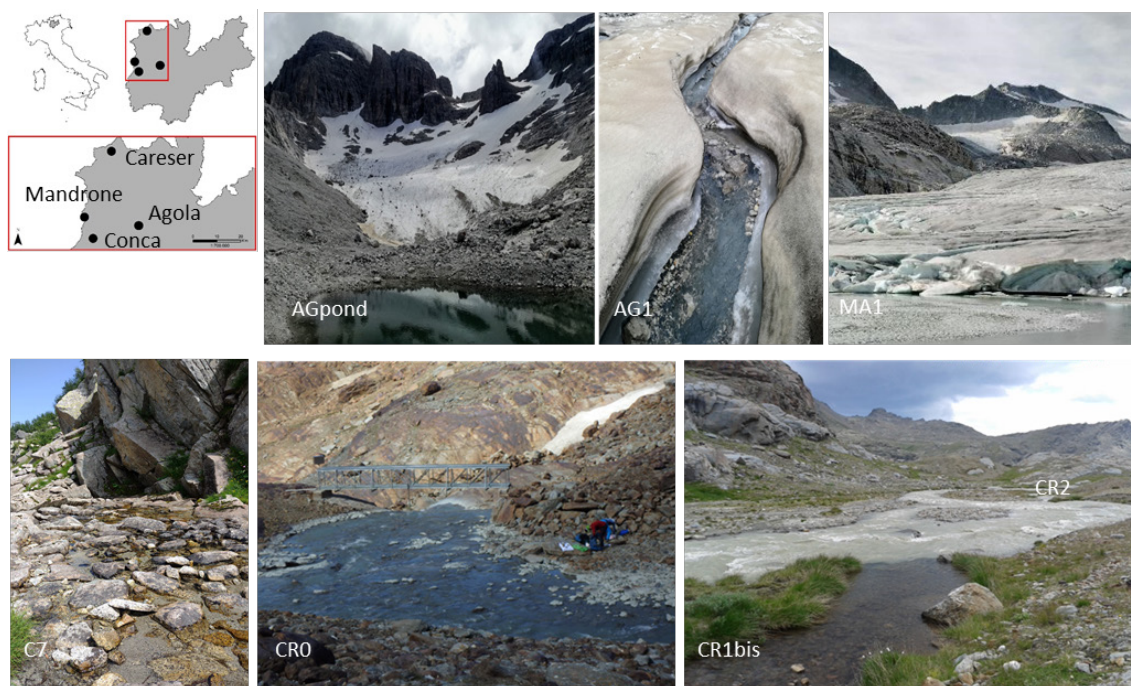


Figure 1. Sampling sites (Northern Italy, Rhaetian Alps, 46°N).

Table 2. Sampling sites features. Glacier surface data from Smiraglia and Diolaiuti (2015). Chl *a* = chlorophyll *a*. GI = Glacial Index.

Sampling site	Stream	Type	Altitude (m a.s.l.)	Distance from the source in 2015 (km)	Feeding glacier surface in 2015 (km ²)	GI	Pfankuch index	Chl <i>a</i> (µg/cm ²)
AG1	Agola	kryal	2623	0	0.53	1	39	0.001
AGpond	Agola	proglacial pond	2596	0.02	0.53	0.95	15	0.067
MA1	Mandrone	kryal	2569	0.05	10.14	0.98	47	0.245
CR0	Careser	kryal	2858	0.75	1.39	0.61	58	0.008
CR2	Careser	glacio-rhithral	2642	2.29	1.39	0.34	44	0.134
CR1bis	Careser tributary	krenal	2645	1.36	-	0	15	2.228
C7	Conca tributary	krenal	2170	1.55	-	0	16	1.221

(site C7) and Mandrone (site MA1) in the Adamello-Presanella Mountain Group, Careser (sites CR0, CR1bis and CR2) in the Ortles-Cevedale Mountain group, and Agola (AG1 and AGpond) in the Brenta Dolomites. All sites are located above the treeline (> 2000 m a.s.l.). Three sites are fed by meltwater (kryal type: AG1, MA1 and CR1), two by groundwater (krenal type: C7 and CR1bis), and two with mixed origin (one glacio-rhithral type: CR2 and a proglacial pond: AGpond). Based on the origin, these sites have different glacial influence, quantifiable as Glacial Index (GI), and calculated by

combining the glacier area with distance from the glacier terminus according to Jacobsen and Dangles (2012). The index varies from 0 (no glacial influence) to 1 (maximum glacial influence). For each site, substrate stability was evaluated using the Pfankuch Index (Pfankuch 1975), which is a visual and subjective index that varies from 15 (maximum stability) to 60 (minimum stability). Primary production was measured as chlorophyll *a* from biofilm (Biggs and Kilroy 2000). Biofilm was collected by scrubbing submerged pebbles of known surface area (3x3 cm²) with a toothbrush.

Samples were filtered in the field using a vacuum pump with glass microfiber filters (Whatman GF/CTM, 1.2 µm). Filters were stored frozen until analysis. In the lab, chlorophyll *a* was extracted with 90% acetone and the concentration was read at 665 nm and 750 nm, according to Steinman et al. (2017). Overall, the sites with the highest glacial influence and the lowest substrate stability were CR0 and MA1, followed by CR2 and AG1 (Table 2). These sites also exhibited the lowest primary production, with the exception of MA1, which had significant presence of large thalli of the crysophyte *Hydrurus foetidus* Villars. The highest primary production was measured in the two krenal sites (CR1bis and C7), where bryophytes were also present.

Sampling of larvae and gut content analysis

Larvae were collected in the morning using a pond net (100 µm mesh size) using the kick sampling technique in five different microhabitats/site for two minutes each. Additional samples were collected using a drift net (100 µm mesh size) for 1 hour in each site. Larvae were preserved in 75% ethanol immediately after sampling. Sorting, species identification, and larval instar confirmation were performed under a stereomicroscope (Leica S Apo 10X-80X coupled with Flexcam C5) after preparing permanent slides in Canada Balsam following separating the gut (see details below) under a compound microscope (Nikon Eclipse Ci, up to 1000x magnification) according to: McCauley (1974), Schmid (1993), Epler (2001), Janecek

(2007), Andersen et al. (2013), Vallenduuk and Pillot (2014), Ferrington and Berg (2019).

Gut content analysis (GCA) was performed on a selection of species, including 13 taxa that represent the most frequent and abundant taxon in these habitats according to Lencioni et al. (2021): *Diamesa bertrami*, *Diamesa latitarsis*, *Diamesa steinboeckii*, *Diamesa zernyi*, *Pseudokiefferiella parva*, *Eukiefferiella minor*, *Metriocnemus eurynotus* gr., *Parametriocnemus stylatus*, *Thienemanniella clavicornis*, *Tvetenia calvescens*, *Macropelopia* sp., *Zavreliomyia* sp., *Micropsectra atrofasciata* gr. Mature larvae (III-IV instar) were available for all species, while early instars (LI and LII) were only available for a few species and only a few specimens were collected. For this reason, we report in this work only the results of the mature larvae, as we are aware of the fact that assigning a trophic group or feeding strategy based on a single larval stage is not sufficient to define the diet of a species. In any case, in our opinion, the data is still of interest for beginning to explore the diet of cryophilic species that have not yet been studied in depth. In Table 3 we report the functional feeding groups (FFG) assigned *a priori* to the 13 taxa according to Moog and Hartmann (2017) (Table 1); however, for *Metriocnemus eurynotus* gr. we based FFG on Pillot (2013).

Guts of 3-4 individuals per taxon were removed, for a total of 72 individuals analysed. We verified that the intestine did not empty when pressed under the cover slip. Proportions of the different

Table 3. Feeding groups assigned to the 13 chironomid taxa according to Moog and Hartmann (2017); the scores assigned to *Metriocnemus eurynotus* gr. were derived from its feeding habits, described by Pillot (2013). The symbol * indicates the major feeding preference while the symbol + indicates a secondary preference. Numbers indicate the score attributed to the feeding group (from 1 to 10).

Taxon	GRA	AFIL	DET	MIN	PRE
<i>Diamesa bertrami</i> Edwards, 1935	*	-	+	-	+
<i>Diamesa latitarsis</i> (Goetghebuer, 1921)	*	-	+	-	+
<i>Diamesa steinboeckii</i> Goetghebuer, 1933	*	-	+	-	+
<i>Diamesa zernyi</i> Edwards, 1933	*	-	+	-	+
<i>Pseudokiefferiella parva</i> (Edwards, 1932)	*	-	+	-	+
<i>Eukiefferiella minor</i> (Edwards, 1929)	8	-	2	-	-
<i>Metriocnemus eurynotus</i> gr.	*	-	*	-	-
<i>Parametriocnemus stylatus</i> (Kieffer, 1924)	*	-	*	-	-
<i>Thienemanniella clavicornis</i> (Kieffer, 1911)	6	-	4	-	-
<i>Tvetenia calvescens</i> (Edwards, 1929)	7	-	3	-	-
<i>Macropelopia</i> sp.	-	-	2	-	8
<i>Zavreliomyia</i> sp.	-	-	-	-	10
<i>Micropsectra atrofasciata</i> gr.	1	1	8	-	-

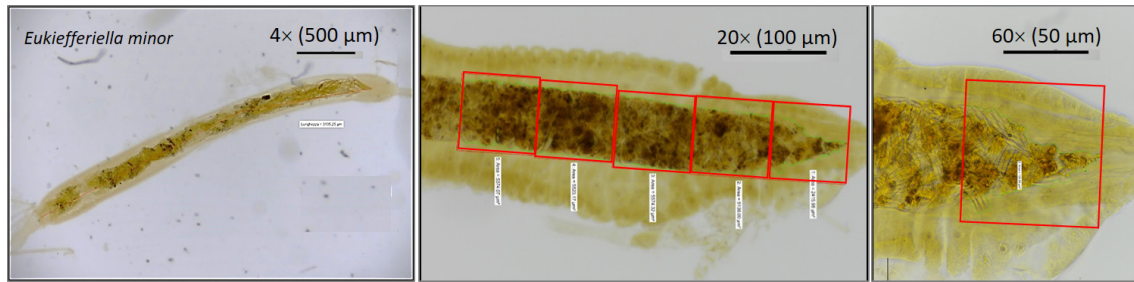


Figure 2. Gut of one IV-instar larvae of *Eukiefferiella minor*. Red frame represents the grid designed with the NIS-BR software. The length of the gut was measured at 4x magnification (on the left), details in each quadrant at 20-60x magnification. The numbers on the white background are the measured lengths and areas, automatically displayed on the image in minute font.

food items were estimated using a 10x10 grid designed with the NIS-BR software (camera DS-Ri2 on Nikon Eclipse) (Fig. 2). Specifically, the total length of the intestine was measured at 4x magnification and then it was virtually divided into ten subsections of equal size (red squares/rectangles in Fig. 2). A photograph was taken of each of these ten squares. The areas occupied by different food categories within each square were identified and measured using magnification of 40x or 60x. The percentage of area occupied by each food category was calculated by first determining the area relative to the sum of all recorded food categories within each gut subsection, and then averaging these percentages across the entire gut following the methodology of Cheshire et al. (2005).

Food items were divided into 10 categories, according to Cheshire et al. (2005): MM = Mineral Material, AT = Animal Tissue, ALG = Algae (except diatoms), DIA = Diatoms, PT = Plant tissue, AD = Amorphous detritus (FPOM), LIC = Lichens, BRYO = Bryophytes, FUN = Fungi (including fungal spores and hyphae), and POL = Pollen. We modified these categories according to Moog & Hartmann (2017) with plant tissue fragments < 1 mm in PT and AD as only FPOM. Food items were associated with FFGs (Table 4). Diatoms were identified according to Barber and Hawthorth (1981) and Hofmann et al. (2011). Beyond diatoms, efforts were made to identify other resistant microalgal structures, utilizing specialized literature on Alpine stream phytoplankton, such as Entwisle et al. (1997), Dillard (1999), Komárek and Anagnostidis (2007, 2008), Komárek (2013), and Cantonati et al. (2015).

Inter-individual, inter-species, and inter-site significant differences ($p < 0.05$) for percentage of food categories were tested with the Mann-Whitney non-parametric U test and one way ANOVA, performed using STATISTICA version 12.0 (@Statsoft).

Results and Discussion

Catalogue of gut contents

The first catalogue of the gut contents of alpine chironomids (e.g., Figs 3-6) includes a long list of algae, most of which were diatoms (Table 5) which was expected as diatoms are generally dominant in headwaters (Bert et al. 2024). The majority of algae with soft structures were unidentifiable due to the rapid digestion of carbohydrates. However, resistant structures like siliceous diatom cell walls persisted. Cells belonging to this group were often found emptied of their contents but with intact skeletons even after expulsion. Similarly, thick-walled cells, including cysts, other resistance structures, or certain green algae (e.g., *Cosmarium*) and a cyanobacteria (e.g., *Chamaesiphon*, very common in glacial habitats), remained undigested despite enzymatic activity. In Alpine streams, significant cyst-forming algae components of the phytoplankton are chrysophytes, specifically *Hydrurus foetidus* and *Phaeodermatium rivulare* (Rott et al. loc. cit.). Therefore, unidentified algal cysts found in this work are likely attributable to one of these two species.

Table 4. Food items categories and associated dietary groups.

Food Categories	Associated FFG
MM – Mineral Material	DET - Detritivores
AT – Animal Tissue	PRE - Predators
ALG – Algae (except diatoms)	GRA – Grazers
DIA - Diatoms	GRA - Grazers
PT – Plant tissue	SHR – Shredders
AD – Amorphous detritus	DET - Detritivores
LIC - Lichens	GRA – Grazers
BRYO – Bryophytes	SHR – Shredders
FUN - Fungi	DET – Detritivores
POL - Pollen	DET – Detritivores

To illustrate the variety of habitat types and food categories from the most abundant species found in different sites, we selected four representative species as examples: *T. calvescens* (from site CR-1bis) (Fig. 3), *P. parva* (from site C7) (Fig. 4), *M. atrofasciata* gr. (from site C7) (Fig. 5), *D. steinboeckii* (from AG1 and MA1), and *D. zernyi* (from CR0 and MA1) (Fig. 6). The gut contents of these four taxa can be seen in Figures 3-5 and show vegetal groups, which are mostly represented in high altitude rhithral and krenal streams (i.e., mosses, thallose chrysophytes), and some of the most common diatom taxa composing the epiphytic communities growing on mosses on circumneutral to slightly acidic waters (i.e., elongated *Fragilaria* spp., *Eunotia* sp., *Odonthidium aff mesodon*, and *Tabellaria flocculosa*) (Rott et al. 2006, Cantonati et al., 2012, Rotta et al. 2018). Pollen grains, fungal spores, and chrysophyte spores were also represented. In contrast, the gut contents in Figure 5 were mainly composed of mineral material and very scarce vegetal cells (chrysophyte cysts of *H. foetidus* and coccal cyanobacteria), thus reflecting the very sparse vegetation and periphytic assemblages characterising kryal streams

Mineral material in some individuals of *Diamesa* spp. comprised 99% of gut contents (Fig. 6). Among the MM, only a few cysts of chrysophytes such as *Hydrurus foetidus* and a few colonies of

Chamaesiphon were observed. We can argue that MM is ingested, not digested by the animal, and then expelled. In environments with significant glacial influence, some MM ingestion could also be involuntary due to high turbidity. We associated the presence of MM in the gut with a detritivorous feeding habit, where organisms likely consume the organic coating on mineral particles. Additionally, larvae might ingest MM for the microorganisms (bacteria, fungi, viruses) associated with it, as also argued by Sharp et al. (1999), Logue et al. (2004), Hodson et al. (2008), and Clitherow et al. (2013). Therefore, for these animals living in habitats with low productivity, bacteria may be an important food source.

Inter-individual variability within the same population

Inter-individual variability was observed within individuals of the same population for all species (Fig. 7). For example, in Figure 7A the comparison between three individuals of *P. parva* collected from the same site (C7) is shown, highlighting that this species preferentially consumes bryophytes, although they were absent in the gut of one specimen (individual 1) where bryophytes were replaced by diatoms (68%). Similarly, *D. zernyi* from C7 (Fig. 7B) consumed diatoms if present, however in one individual, amorphous detritus

Table 5. List of diatoms identified in larval gut of chironomids collected in four study sites belonging to three habitat types.

	C7 (krenal)	CR1bis (krenal)	CR2 (glacio-rhithral)	AGpond (proglacial pond)
<i>Achnantes</i> sp.	x		x	x
<i>Achnantidium minutissimum</i>	x	x		
<i>Aulacoseira</i> sp.	x			
<i>Brachysira</i> sp.		x		
<i>Caloneis</i> cf. sp.		x		
<i>Cymbella</i> sp.	x	x	x	
<i>Cymbopleura</i> sp.		x		
<i>Diatoma</i> cf. <i>mesodon</i>	x	x		
<i>Diatoma</i> sp.	x	x		
<i>Eunotia</i> sp.	x	x	x	
<i>Fragilaria arcus</i>		x		
<i>Fragilaria</i> sp.	x		x	
<i>Fragilaria ulna</i>		x		
<i>Gomphonema</i> sp.	x	x	x	
<i>Nitzschia</i> sp.	x	x		
<i>Pinnularia</i> sp.		x		
<i>Tabellaria</i> sp.	x	x		

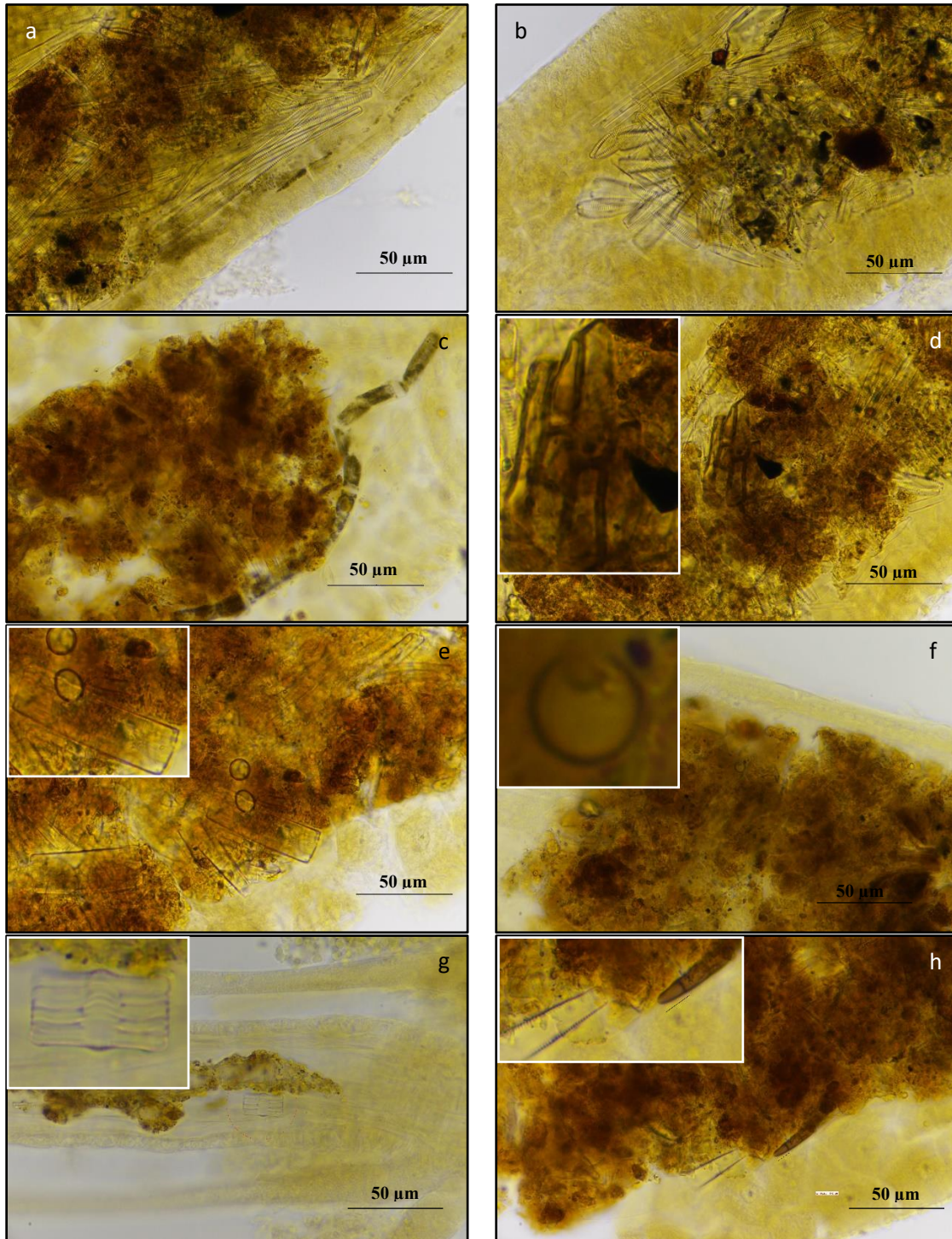


Figure 3. *Tvetenia calvescens* (site CR1bis). a. *Fragilaria aff. ulna* (DIA); b. *Gomphonema* sp. and *Fragilaria* sp. (DIA); c. cf *Klebsormidium rivulare* (ALG); d. Plant tissue (PT); e. Chrysophyte cysts (ALG) and *Eunotia* sp. (DIA); f. Chrysophyte cyst (ALG); g. *Tabellaria flocculosa* (DIA); h. Fungal spores (FUN) and *Gomphonema* sp. (DIA).

was the dominant food type. In *T. calvescens* (Fig. 7C) amorphous detritus was the dominant food type consumed by two specimens but a third specimen consumed more diatoms. Intra-specific differences in gut content of chironomid larvae were observed also by other authors (e.g. Lemes-Silva

et al. 2014). The frequently observed significant inter-individual dietary variation was addressed by some authors as being shaped by resource availability at the microhabitat level (e.g. Lemes-Silva et al. 2014) and by intra-specific competition for food by others (Wiley 1981).

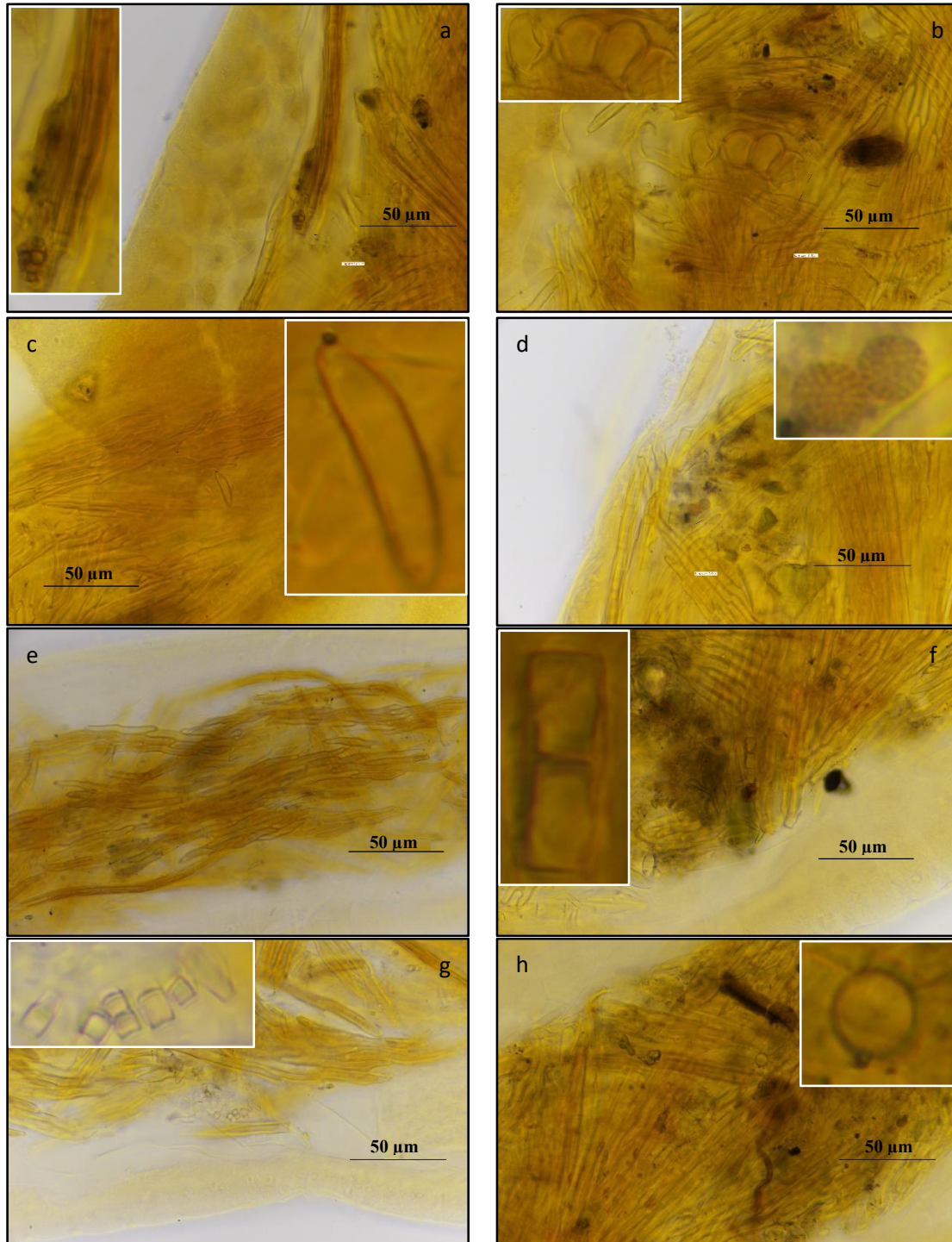


Figure 4. *Pseudokiefferiella parva* (site C7). a. Filamentous cyanobacterium (ALG); b. Plant tissue with empty cells of unidentified green algae (PT, ALG); c. *Eunotia* sp. (DIA); d. Pollen grains (POL); e. Moss (MOS); f, g. *Odonthidium* aff. *mesodon* (DIA); h. Chrysophyte cyst (ALG).

Inter-species variability from the same habitat type

Significant differences were observed between species living in the same habitat type and classified *a priori* (i.e., based on Moog and Hartmann, 2017) into the same feeding group (e.g., detritivorous, grazer, or predator). In Figure 8 we provide

an example of five grazer-detritivorous (GRA-DET) species collected in the krenal site CR1bis. According to our analysis, *D. zernyi* and *P. stylatus* can be classified as DET-GRA, *E. minor* as GRA-DET, *P. parva* as GRA-DET-SHR (SHR = shredder; with bryophytes representing 53% of ingested

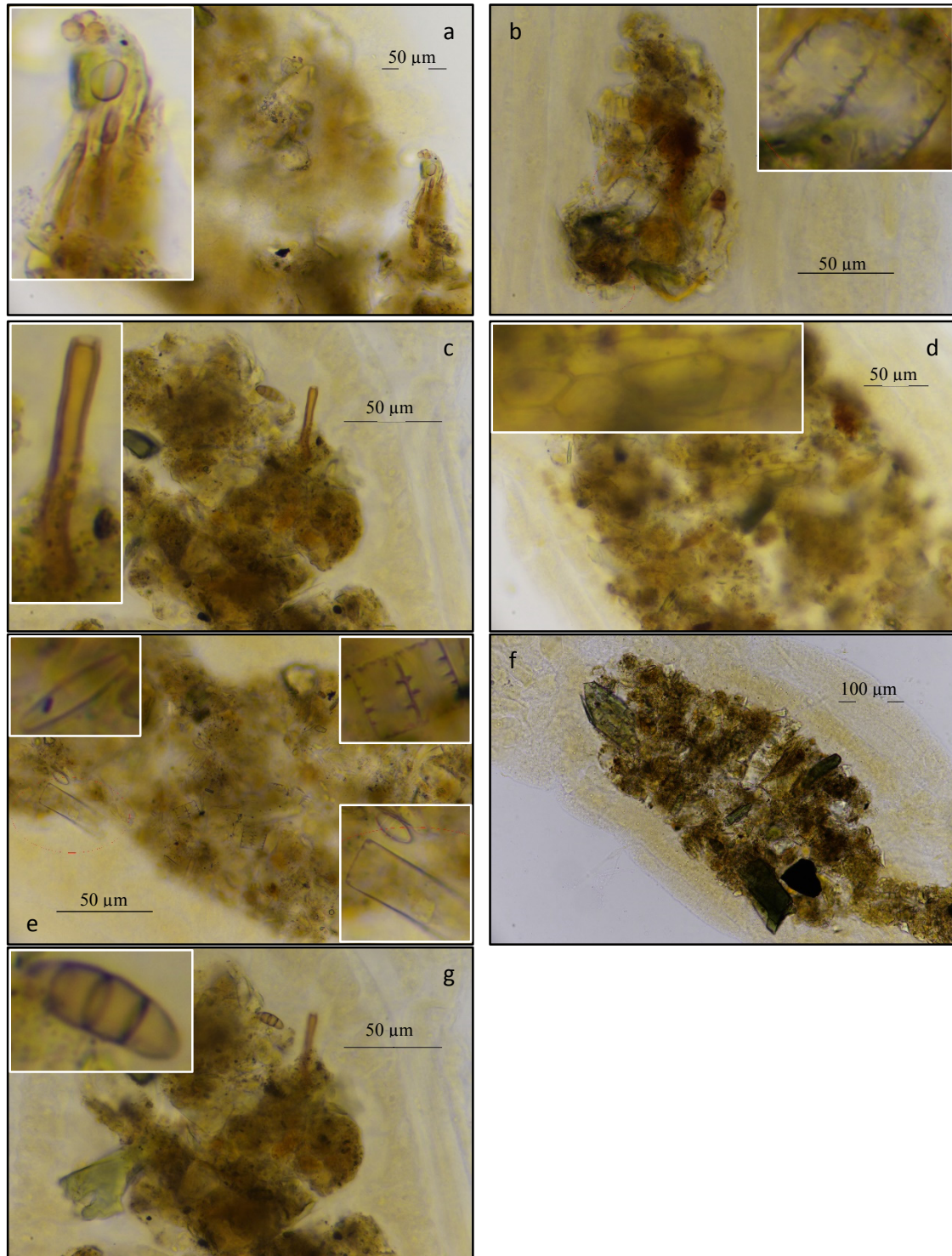


Figure 5. *Micropsectra atrofasciata* gr. (site C7). a. Filamentous cyanophyte (ALG); b. *Diatoma* sp. (DIA); c. Fungal hypha (FUN); d. Plant tissue (PT); e. On the top left *Achnanidium minutissimum*, on the top right *Diatoma* sp. and on the bottom right *Eunotia* sp. (DIA); f. Mineral material (MM) and amorphous debris (AD); g. Fungal spores (FUN).

food), and *T. calvescens* as DET-GRA-SHR (also eating plants, fungi pollen and lichens, altogether 5% of the gut content). Amorphous detritus was much more prevalent in *D. zernyi* and *P. stylatus* than in the other species, whereas *P. parva* seems to prefer bryophytes and can also behave as a

shredder which differs from its *a priori* categorisation (Table 3). These results suggest that, at least for IV instar larvae, species sharing the same habitat type or site and generally classified within the same trophic category may exhibit different diets (with high inter-individual variability, e.g., Fig. 7).

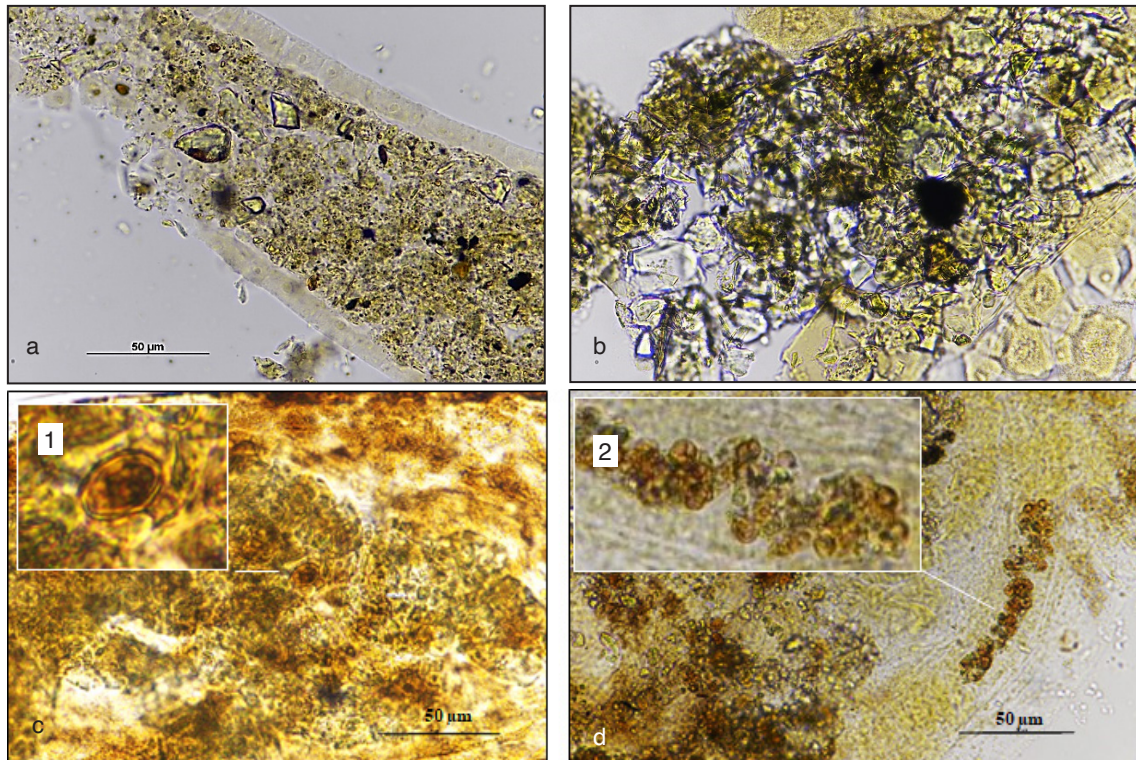


Figure 6. a. *Diamesa zernyi*. Mineral material (MM) and amorphous debris (AD) from site CR0; b. *Diamesa zernyi*. Mineral material (MM) and amorphous debris (AD) from site MA1; c. *Diamesa steinboeckii*. 1) *Hydrurus foetidus* cyst (ALG) from site MA1 and d. 2) *Chamaesiphon* sp. (Cyanobacteria) (ALG) from site AG1.

Inter-habitat type variability within the same species

Larvae of the same species living in different types of habitats have gut contents with significantly different percentages of food categories. This was observed for most species. For example, larvae of *D. zernyi* (Fig. 9) living in kryal habitats have very similar stomach contents, dominated by MM followed by AD. Although not significant, the highest percentage of MM was observed in larvae from the CRO site, which was where the lowest primary production levels were measured (Table 2). However, in the gut of larvae collected in C7, diatoms significantly prevailed, suggesting that where diatoms are available, *D. zernyi* will feed preferentially on them. These differences between individuals of the same species from different habitats emphasize opportunistic behavior and suggest some flexibility in the feeding habitats in these species.

Conclusion

We assessed food item preferences according to taxonomy and habitat type with different primary production and we assume different algal abundance and composition. It is interesting to note that individuals belonging to the same species can be opportunistic and exhibit different diets in dif-

ferent habitat types. Opportunism is expected to be more frequent in glacier-fed streams than in groundwater-fed and/or downstream reaches with a broader array of resources available, which can better support specialist feeding behaviours (Sertić Perić et al., 2021). Generally, if diatoms are present, all chironomid species eat them, probably due to their high nutritional quality. In fact, based on the composition and concentration of fatty acids, diatoms are characterized as potentially excellent food resources, whereas other groups, such as chrysophytes and green algae are characterized as intermediate and cyanobacteria as low-quality food resources for herbivores in freshwater habitats (Taipale et al. 2013). Algal nutritional quality is generally of high importance for the fitness of consumers and for sustaining stream food webs (Guo et al. 2016, Niedrist et al. 2018).

Overall, the diet (based on what was present in the gut of late instar larvae) and feeding group of the different species were reviewed. A certain trophic flexibility and omnivory was found, which may facilitate the adaptation of chironomids to changes in available resources due to glacier retreat.

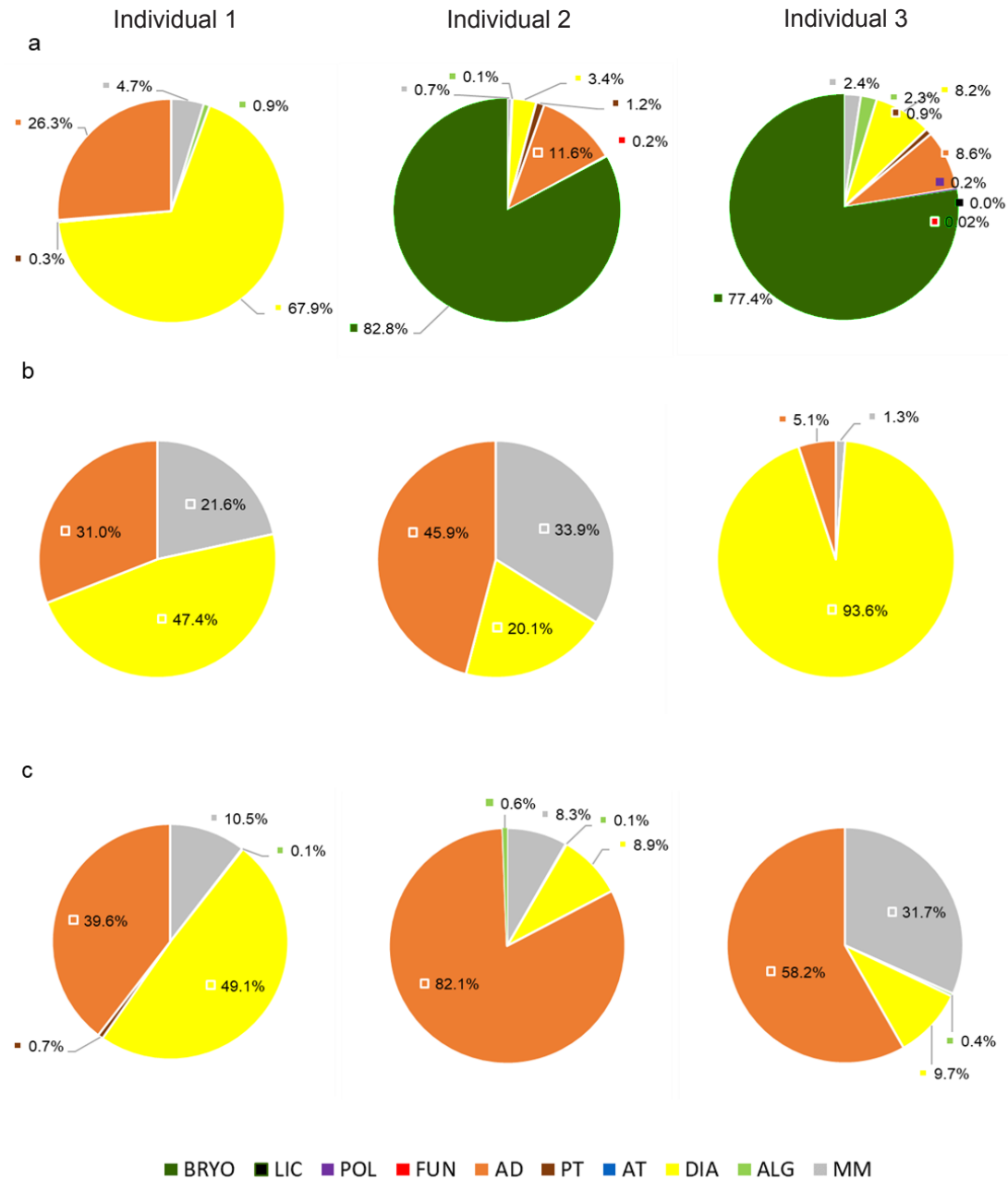


Figure 7. Inter-individual variability observed in three individuals of the same species from the same site (C7). Numbers in the legend refer to the 10 food items reported in Table 3. a. *P. parva* larvae from site C7; b. *D. zernyi* from C7; c. *T. calvoscens* from CR1bis. MM = Mineral Material, AT = Animal Tissue, ALG = Algae (except diatoms), DIA = Diatoms, PT = Plant tissue, AD = Amorphous detritus, LIC = Lichens, BRYO = Bryophytes, FUN = Fungi (including fungal spores and hyphae) and POL = Pollen.

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The first author dedicates this article to her friend and mentor, Len C. Ferrington Jr.

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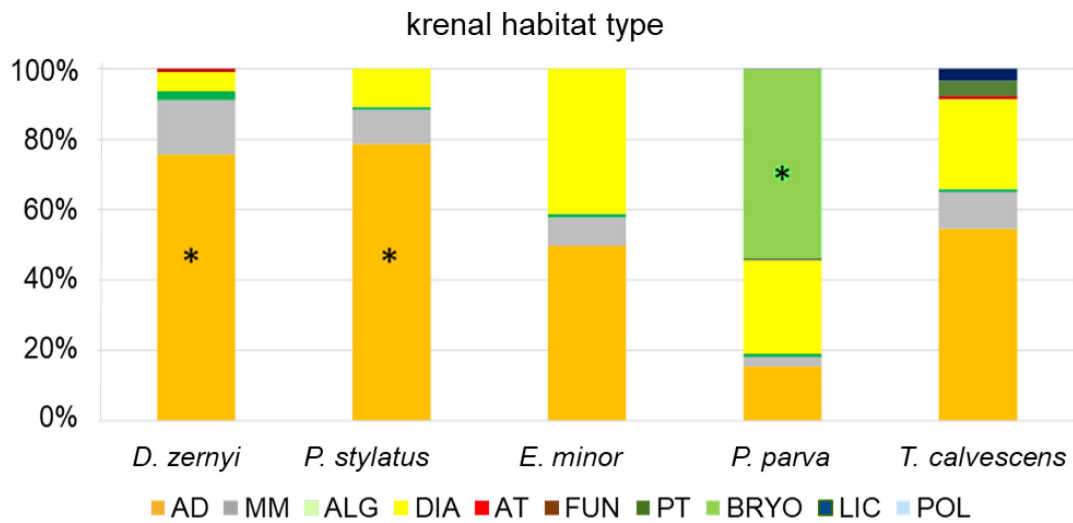


Figure 8. Relative composition of gut contents in five species from a krenal habitat type (site CR1bis). * = significant different food items ($p < 0.05$). AD = Amorphous detritus, MM = Mineral Material, ALG = Algae (except diatoms), DIA = Diatoms, AT = Animal Tissue, FUN = Fungi, PT = Plant tissue, BRYO = Bryophytes, LIC = Lichens, POL = Pollen. For each species, $n=3$ specimens were examined.

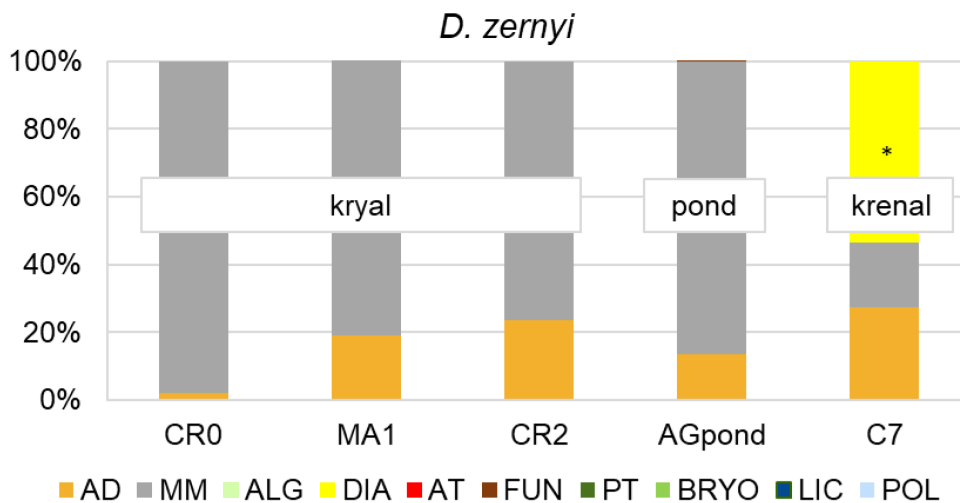


Figure 9. Diet of *Diamesa zernyi* from different sites and habitat types. CRO, MA1 and CR2 = kryal; AGpond = proglacial pond; C7 = krenal. * = significant different food item ($p < 0.05$). AD = Amorphous detritus, MM = Mineral Material, ALG = Algae (except diatoms), DIA = Diatoms, AT = Animal Tissue, FUN = Fungi, PT = Plant tissue, BRYO = Bryophytes, LIC = Lichens, POL = Pollen. For each site, $n=3$ specimens were examined.

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