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ORIGINAL PAPER

The influence of depth and macrophyte habitat on paleoecological studies using chironomids: Enol Lake (Spain) as a case study

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Abstract Paleolimnological studies often rely on a single sediment core for reconstructing past environmental changes of an entire lake system. This involves a number of assumptions about the correct representativeness of the living assemblage by the subfossil assemblage. This paper is aimed at understanding the main drivers affecting the dispersion and transportation of Chironomidae head capsules, which may affect the correct interpretation of downcore changes through overrepresentation or underrepresentation of certain taxa. We analyzed the chironomid living assemblage of Enol Lake (Picos de Europa National Park, Spain) and compared the subfossil assemblage at different depths. We found a highly homogeneous composition and density of recent subfossil assemblage along the depth transect (i.e. dominance of the Tanytarsini *Paratanytarsus austriacus*-type), which would indicate that a single core retrieved at any depth would be representative of the lake community. However, the composition of the benthic living assemblage changed significantly with depth, suggesting the existence of a driving force behind the dominance of *P. austriacus*-type in the subfossil assemblage. We argue that the dense mats of Characeae present in the sublittoral area (from 2 to 8 m) are most likely responsible for this homogenization, since this is the preferred habitat of *Paratanytarsus*, which was found at very high densities at this depth. Thus, we conclude that the interpretation of past changes in the lake conditions should be made with caution due to the overrepresentation of *P. austriacus*-type head capsules along the depth transect. Our findings show that it is important to explore the relationship between the living and the recent subfossil fauna of each lake in paleolimnological studies, since understanding deposition and transport patterns can help to avoid misinferring past environmental and limnological conditions.

Keywords Chironomidae · Head capsules · Transport · Deposition · Characeae

Maria Rieradevall: Deceased.

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Introduction

Paleolimnological studies often rely on a single sediment core for reconstructing past environmental changes of an entire lake system. This involves a number of assumptions about the similarity in composition and abundance between the living and the subfossil assemblage (van Hardenbroek et al. 2011). Moreover, this single core is usually retrieved in the lake centre, as it is believed to record all the processes and remains originated from the entire lake basin (Smol 2008). This assumptions holds for a variety of proxies, including Chironomids (Insecta: Diptera), which have been traditionally used in paleolimnology due to their abundance, ubiquity, and the good preservation of their chitinous larval remains (Walker 2001). Chironomid living assemblages may experience great spatial and temporal changes, which are mainly related to different habitat preferences (Frey 1988; Eggermont et al. 2008), changes in the emergence patterns (Heinis and Davids 1993), and other ecological traits (dispersion, predation, competence, etc.). Depth has been usually considered a key variable that helps to explain chironomid distribution (Lindegaard 1992; Korhola et al. 2000; Brooks et al. 2007) because it is strongly linked to several factors that affect chironomid composition and diversity (e.g.: temperature, oxygen, pH, substrate, aquatic vegetation, etc.) (Prat and Rieradevall 1995; Brodersen and Quinlan 2006; Kurek and Cwynar 2009). Thus, this spatial and temporal heterogeneity could lead to a poor representation of the overall Chironomidae community by a single core retrieved from the lake centre.

Subfossil chironomid remains are considered to represent the living assemblage at the moment of the sediment deposition. However, once chironomids die or moult, different diagenetic and transport processes can alter the composition of subfossil remains. In general, these processes are mainly driven by three factors: (1) lake morphology (Frey 1988; Schmäh 1993) and substrate composition (Heiri 2004), (2) species morphology and taphonomy (Walker et al. 1984), and (3) environmental factors, mainly wind (Frey 1988; Holmes et al. 2009) and currents (Bigler et al. 2006; Luoto 2010). All these factors indicate that each lake may respond individually and heterogeneously to these processes, as their chironomid assemblage composition differ from one to another, as well as their morphological and environmental characteristics. Moreover, such processes may affect certain taxa more strongly than others, leading to over- or underrepresentation of certain taxa (Frey 1988; Brodersen and Lindegaard 1999; Eggermont et al. 2007). In fact, redeposition processes by sediment erosion and transportation are considered one of the most important sources of disturbance of chironomid remains (Kansanen 1986), which may lead to a misinterpretation of the environmental factors shaping subfossil assemblages.

Since each lake has distinctive geomorphological and environmental characteristics, many authors have claimed that each lake should be studied separately to disentangle the local processes that affect the subfossil assemblage used for interpreting past environmental changes (Frey 1988). Ideally, the study of the subfossil assemblage should be complemented with information on the living assemblage to obtain complete and reliable information to infer past changes (van Hardenbroek et al. 2011). However, only a few studies have explored the relationship between living and subfossil chironomid assemblages, leading to contradictory results. Whereas some studies found that most subfossil chironomids tend to remain where the larvae lived (Iovino 1975; Walker et al. 1984), van Hardenbroek et al. (2011) found that the remains are transported and redeposited offshore. The same contradictory patterns have been showed by studies focusing exclusively on the subfossil assemblage: whereas several studies found significant changes of the subfossil assemblage with depth (Frey 1988; Heiri et al. 2003; Heiri 2004; Kurek and Cwynar 2009; Luoto 2010; Cao et al. 2012; Karmakar et al. 2014), others (Frey 1988; Schmäh 1993; Brodersen and Lindegaard 1999; Eggermont et al. 2007; Langdon et al. 2008; Holmes et al. 2009) did not found any significant depth pattern.

The main objective of this study was to understand the relationship between the living and recent subfossil Chironomidae assemblage of Enol Lake (Northwestern Spain). In particular, we aimed to explore the presence and relative abundance of midge remains along the depth transect, as well as to elucidate at which depth the subfossil assemblage best represents the whole community. Previous studies in Enol Lake (Tarrats et al. 2017) have shown that the living chironomid assemblage changes significantly along depth, with three main groups: (1) littoral (0–2 m), (2) *Chara*-related (2–8 m), and (3) profundal (8–22 m).

We expected that two contrasting patterns could emerge from our results: (1) most of the species would remain in the same lake depth zone, and (2) some or many species would be transported to other lake zones. According to the first pattern, the subfossil assemblage would be reliable to infer past environmental and limnological conditions, but different cores would have to be retrieved in different zones to ensure a good representation of the overall living assemblage. According to the second pattern, a single core would accurately represent the whole living assemblage, but the over- or under- representation of certain taxa could lead to misleading inferences of past environmental and limnological conditions.

Study site

Enol Lake (43°16′N, 4°59′W, 1070 m asl) (Fig. 1) is a karstic lake of glacial origin located in the northwestern part of Spain (Asturias), in the western massif of Picos de Europa National Park. It has a water surface of 12.2 ha, a maximum depth of 22 m and a small watershed (1.5 km^2). The lake is fed by groundwater and surface runoff and it has no permanent inlets. Water loses occur through evaporation, groundwater discharges and an outlet located at the northeast border of the lake, which is regulated by a small dam. Previous surveys (Velasco et al. 1999; Moreno et al. 2011) and the data collected in our study characterize the lake as warm monomictic (with a thermocline located between 7 and 12 m from early July until early November). The lake is oligotrophic (total phosphorous 8 μg l^{-1}, Chl-a 0.5–1 μg l^{-1}), moderately hard (alkalinity 2.4 meq l^{-1} and 24–37 mg Ca l^{-1}) and with a conductivity ranging between 150 μS cm^{-1} at the surface and 227 μS cm^{-1} at the bottom. It is almost fully covered with a dense carpet of *Chara* sp. between 2 and 8 m of depth, while *Potamogeton* sp. occurs between 1 and 3 m depth. Despite this oligotrophy the bottom of the lake is anoxic during 4–6 months every year during the stratification period (García-Criado and Martínez-Sanz 2010).

Methods

Sampling and laboratory procedures

Surface sediment sampling of Enol Lake was performed in two different campaigns: (1) July 2013 and (2) July 2014. The surface samples for studying the subfossil assemblage correspond to the topmost (0–1 cm) of the sediment, and their subfossil assemblage composition is considered to be analogue of the modern assemblage (Frey 1988). We collected 3 samples per depth following a depth transect every

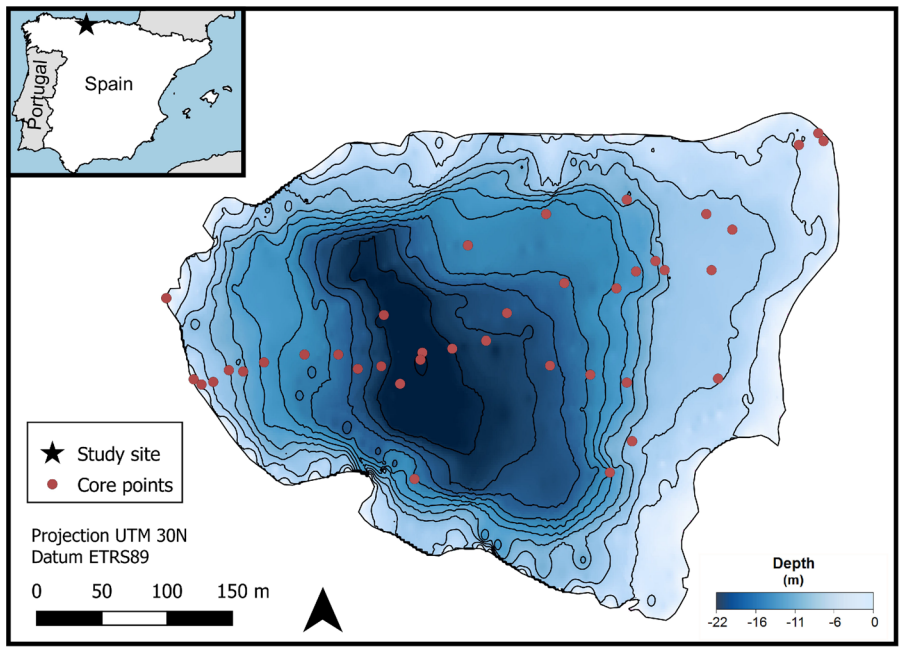

Fig. 1 Enol Lake location map showing sampling points for recent subfossil chironomid assemblage analysis. Bathymetry adapted from Rodríguez-García et al. (2016)

4 m (at 4, 8, 12, 16 and 20 m) in July 2013, and every 2 m of depth following two transects in July 2014 (Fig. 1). By that, we aimed to cover the whole spatial variability, either longitudinal or transversal. Surface sediment samples for subfossil midge analysis were taken using a UWITEC gravity corer. The first centimetre of each core was subsampled in the field using a UWITEC core cutter and the material was transferred to zip bags and preserved in the refrigerator until its analysis. The laboratory protocol for the subfossil samples followed a standard procedure (Walker 2001): (1) wet sediment was weighted, deflocculated in warm KOH (70C°) and stirred at 300 rpm for 20 min; (2) the sediment was sieved through a 90 µm mesh size sieve; (3) Chironomidae head capsules were picked out under a stereo microscope at 40× magnification, dehydrated in 96% ethanol and mounted on microscope slides using Euparal®; (4) Chironomidae head capsules were identified under an optical microscope (Olympus CX41) at 400× magnification using several specialized guides (Wiederholm 1983; Rieradevall and Brooks 2001; Brooks et al. 2007).

Living chironomid larvae samples came from 8 sampling campaigns performed between 2013 and 2014 in May, July, September and November of each year. These samples included 3 littoral samples per campaign and 3 replicates per depth every 2 m per campaign. Littoral samples were collected using the kick-sampling method (sampling surface: 1 m^2) with a 250-µm mesh net. In the case of the sublittoral and profundal zones (2–22 m), an Eckman grab was used (sampling surface: 225 cm^2), and the samples were sieved in the field using a 250 µm mesh net and preserved in formaldehyde at 4%. For each sample, we picked up all the Chironomidae larvae present to a maximum of 300 individuals, which were firstly sorted by morphotypes. A minimum of 50 larvae of each morphotype were treated with 10% potassium hydroxide (KOH) at 70 C° and, after dehydration, were mounted on microscope slides in Euparal®. The Chironomidae specimens were identified using an optical microscope (Olympus CX41) at 400× magnification and several taxonomic keys (Wiederholm 1983; Rieradevall and Brooks 2001; Brooks et al. 2007). Once morphotypes were identified, the most abundant taxa were counted directly from samples without further processing. The identification of larvae was validated through the examination of a large collection of pupal exuviae from the lake using the key of Langton and Visser (2003). The results of this study can be found in Tarrats et al. (2017).

Data analysis

We merged living and subfossil data matrices by defining equivalent taxa in living and subfossil samples (ESM1). This required some arrangements. For example, as we could not identify all subfossil Pentaneurini tribe to genus level due to head capsules bad preservation, we decided to combine the living identified larvae *Ablabesmyia (Ablabesmyia) monilis* (Linnaeus, 1758) and *Zavrelimyia* sp. into a single category (Pentaneurini). Many authors have already emphasized the difficulty to identify some chironomid subfossil taxa, specially Tanypodinae (Walker et al. 1984), due to bad preservation of head capsules (Brooks et al. 2007; van Hardenbroek et al. 2011). Rare taxa, i.e. those that did not reach a relative abundance of $\geq 2\%$ in at least two samples, were removed from all analyses.

We performed a Detrended Correspondence Analysis (DCA) to explore the distribution patterns of both living and subfossil samples. We chose between linear or unimodal-based methods by estimating the lengths of the compositional gradients (i.e. axes 1 and 2). If the length of the gradients is < 2 SD, linear methods (Principal Component Analysis, PCA) are recommended, whereas if the length is > 4.0 SD, unimodal methods (Correspondence Analysis, CA) should be used (Legendre and Legendre 1998; ter Braak and Šmilauer 2002). Given that the first two axes were 2.4 and 1.3 SD respectively, a PCA was performed on Chironomidae relative abundances using the software CANOCO version 4.52 (ter Braak and Šmilauer 2002).

We performed Pearson correlation tests between the average relative taxon abundances of the subfossil assemblage at every depth and the whole average relative taxon abundances of the living assemblage to explore if the subfossil samples were appropriately explaining the total current assemblage. The same correlation analysis was performed to understand the representativeness of a single sample as a reference to the selection of the coring point in paleolimnological downcore studies. In this case, we performed Pearson correlation tests between the average relative taxon abundances of the subfossil assemblage at every depth

with the whole average relative taxon abundances of the subfossil assemblage.

The comparison between the concentrations of living taxa and subfossil remains was plotted using the software Psimpoll (Bennett 2009). In order to understand the relationship between the larvae and the subfossil remains, as well as to understand the transport and deposition of the different taxa, we developed a 'transport index'. This index compares the difference between the abundance of larvae and head capsules for each taxon at every depth category. These categories were established following the different significant groups observed in the living assemblage (Tarrats et al. 2017): (1) Littoral, (2) *Chara* zone and (3) profundal. We calculated percentages of each taxon per depth in relation with its total concentrations along the depth transect. Positive values of this index are related to an overrepresentation of larvae, whereas negative values are related to an overrepresentation of head capsules.

Results

A total of 5500 chironomid head capsules and 14,000 chironomid larvae were identified, belonging to 4 subfamilies (Chironominae, Orthocladiinae, Tanypodinae and Prodiamesinae). We identified 24 taxa in the case of subfossil chironomids, belonging to 21 genera, and 26 taxa in the case of living larvae, belonging to 24 genera. Overall, both subfossil and living communities were similar in terms of taxonomic composition (ESM1). Most taxa were identified both in the living and the subfossil assemblages; exclusive taxa for any of these assemblages were rare (did not reach 2% in at least 2 samples). Thus the assemblage composition of both living and recent subfossil chironomids can be considered as close analogues.

Community ordination and correlation

The PCA using all samples (Fig. 2) explained 49.1 and 12.1% of variance in axes 1 and 2, respectively. Living assemblage samples were arranged according to depth in the first axis, with *Chironomus (Chironomus) plumosus* (Linnaeus 1758) showing a clear preference for deeper zones when compared with the rest of the taxa. The second axis was mainly related with the abundances of *Cladotanytarsus (Cladotanytarsus) atridorsum* (Kieffer 1924), *Paratanytarsus bituberculatus* (Edwards 1929), *Corynoneura lobata* (Edwards 1924) and *Endochironomus albipennis* (Meigen 1830). The subfossil assemblage showed very little dispersion in the PCA, especially for the first axis, and no depth pattern could be observed. In fact, the sample scores indicated that all subfossil samples were strongly related to the littoral and sublittoral living samples located between 0.5 and 6 m of depth.

We found significant differences in the relative abundances of living and surface subfossil midges (Table 1), when samples are grouped according to its location in the littoral, *Chara* or profundal zone. The living assemblage showed a clear depth arrangement, with *Cladotanytarsus*, *Paratanytarsus* and *C. plumosus* dominating the littoral, *Chara* and profundal zones, respectively; whereas the subfossil assemblage was dominated by *Paratanytarsus* all along the depth transect. However, we found a relatively strong correlation between the recent subfossil assemblage at each depth and the overall living assemblage (Fig. 3a). The Pearson correlation r values were relatively high (i.e. ranging between 0.6 and 0.8) and significant (p values ranging between 0.0001 and 0.008) at all depths except at 10 m ($r = 0.4$; $p = 0.11$). The correlation between the recent subfossil assemblage at every depth and the overall subfossil assemblage (Fig. 3b) was strong (0.8–0.98) and significant ($p = 1 \times 10^{-5} - 0.001$), although it decreased at 2 and 10 m ($r = 0.7$; $p = 0.001$).

Taxa deposition

Although the overall recent subfossil and the living assemblages were relatively similar in terms of taxa composition, large differences emerged when looking at the depth distribution of taxa densities (Fig. 4). The transport index showed 3 main patterns related with differences in the deposition of subfossil taxa along the depth transect (Fig. 5). The first was characterized by taxa with a balanced ratio between head capsules and larvae along all zones, suggesting a low transport range (i.e. transport index values around 0). Within this group we found taxa with different depth preferences: some taxa [e.g. *C. plumosus* and *Stictochironomus sticticus* (Fabricius 1781)] were deposited along the whole depth transect, whereas others were almost constrained to the *Chara* zone [*E. albipennis* and *Polypedilum (Polypedilum) nubeculosum* (Meigen,

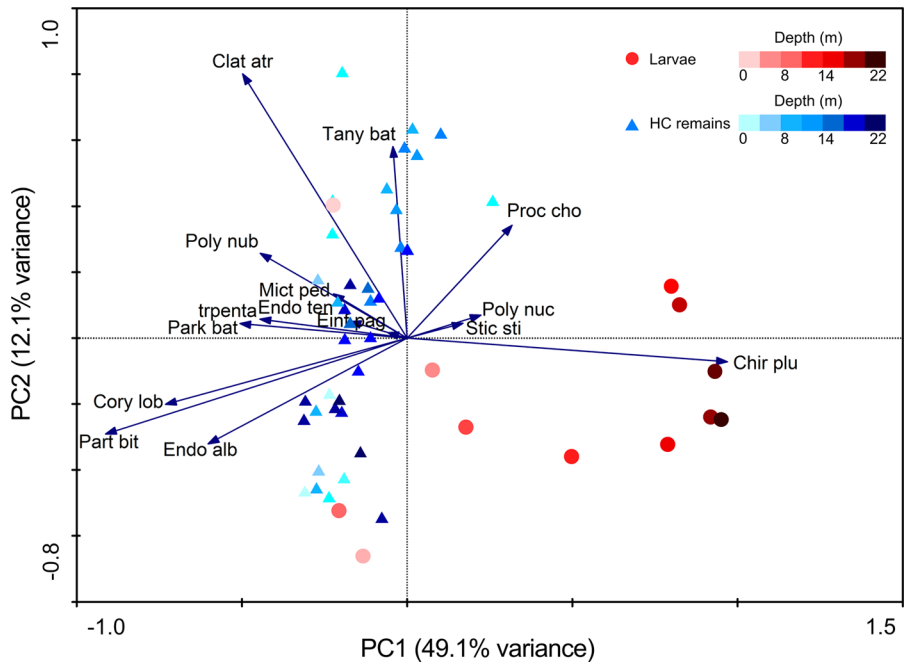

Fig. 2 PCA analysis representing living and subfossil chironomid assemblages of Enol Lake. Red circles represent living samples, following a colour gradation from light red (littoral samples) to dark red (lake bottom samples). Blue triangles represent recent subfossil samples, following a colour gradation along the depth transect, from light blue (littoral samples) to dark blue (lake bottom samples). Taxa codes can be found in ESM1 following Schnell et al. (1999). (Color figure online)

Table 1 Relative abundance of most abundant living and subfossil taxa for each significant zone identified in the living assemblage (Tarrats et al. 2017): (1) littoral, (2) *Chara*, and (3) profundal

Zone	Taxa	Living (%)	Subfossil (%)
Littoral	*Cladotanytarsus*	**31.6**	4.4
	Paratanytarsus	24.1	**46.3**
	Microtendipes	10.7	12.8
	Stictochironomus	9.3	3.5
	Corynoneura	7	2.7
Chara	*Paratanytarsus*	**50.5**	**49.3**
	E. pagana	22.5	7
	E. albipennis	14	10.1
	Tanytarsus	3.3	2.9
	Corynoneura	2.5	9.6
Profundal	*C. plumosus*	**66.8**	4.5
	Paratanytarsus	6.6	**38.7**
	Procladius	6.6	3.4
	Tanytarsus	6.2	7.7
	E. pagana	5.8	8

The most relatively abundant taxa at each zone are shown in bold

1804)]. The second pattern consisted of taxa occurring almost exclusively as living larvae in the littoral zone, which were transported and deposited to deeper levels.

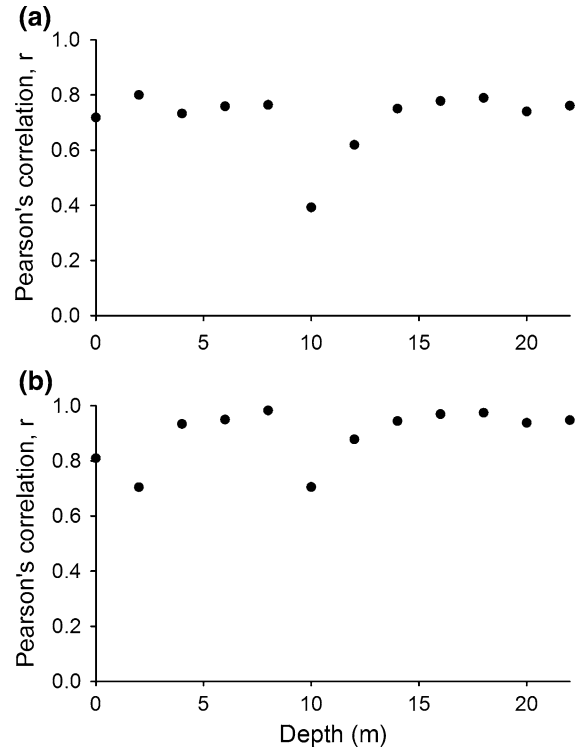

Fig. 3 Pearson correlation r values of **a** subfossil assemblage at every depth versus living overall assemblage and **b** subfossil assemblage at every depth versus subfossil overall assemblage

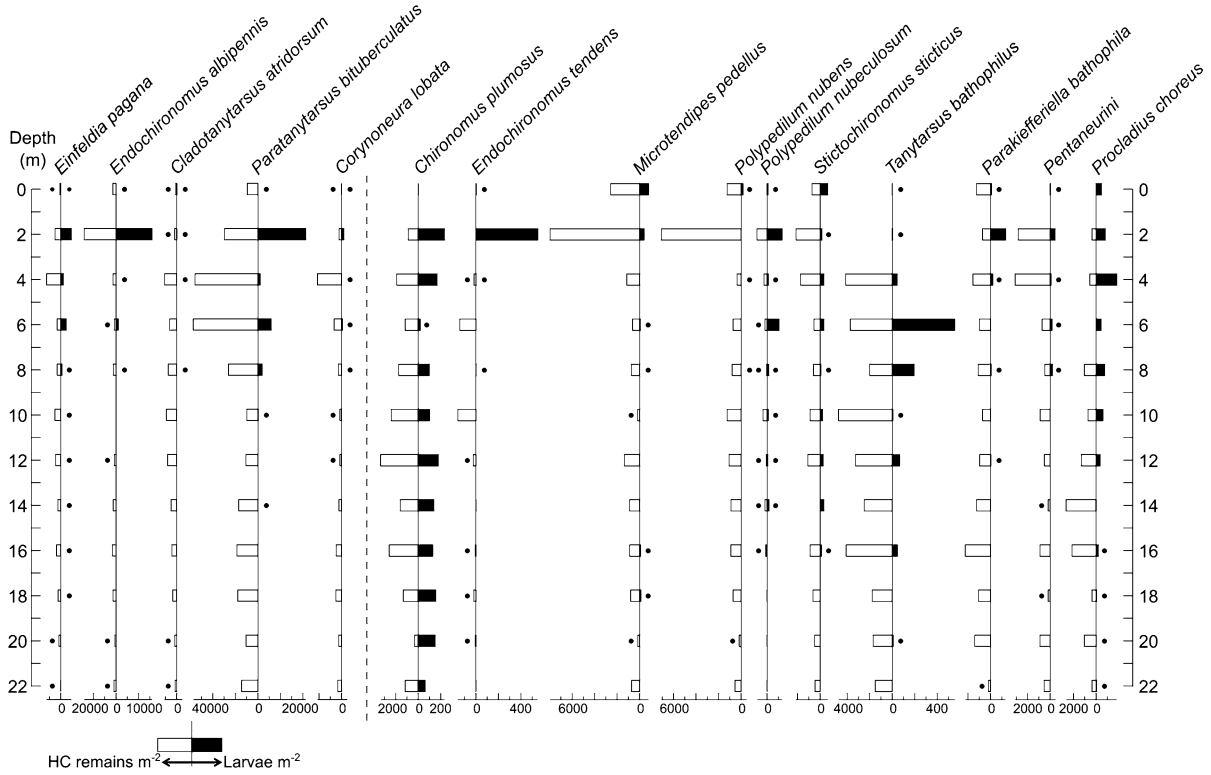

Fig. 4 Comparison between concentration of head capsule remains (white) and larvae (black) from Enol Lake at different depths. Taxa labels follow the living assemblage nomenclature

In this group, two patterns could be observed: (1) taxa that were deposited along the depth transect, showing a deeper transport range (e.g. *Cladotanytarsus*), and (2) taxa that were almost completely deposited in the *Chara* zone, showing a shorter transport range [e.g. *P. nubens* and *Microtendipes pedellus* (De Geer, 1776)]. The third pattern consisted of taxa with the highest living larvae abundances in the *Chara* zone, which were mainly deposited in the profundal zone [e.g. *Parakiefferiella bathophila* (Kieffer, 1912), *Endochironomus tendens* (Fabricius, 1775), *Tanytarsus bathophilus* (Kieffer, 1911) and *Procladius (Holotanypus) choreus* (Meigen, 1804)] or along the depth transect (e.g. *P. bituberculatus*, *C. Lobata*, Pentaneurini tribe).

Discussion

The similarity between the overall living and subfossil assemblages in terms of taxonomic composition makes Enol Lake a good case study for exploring possible transport and deposition processes of chironomid head capsules. According to our results, none of the initial patterns was completely registered. On one side, the subfossil assemblage of Enol Lake had a relatively homogeneous composition along the depth transect. This suggests that a single core retrieved at any part of the lake (except at 0.5, 2 and 10 m of depth) could properly explain the whole assemblage. Moreover, we found that the recent subfossil assemblage was properly representing the overall living assemblage (except at 10 m of depth, mainly due to the low head capsules (HC) abundances of *E. albipennis* found at this level). This is an important finding, since assessing the ability of a single core to properly represent the whole assemblage should be a prerequisite to any paleolimnological study. Concordantly, other studies that did not find any depth-related pattern or threshold of the recent subfossil assemblage (Schmäh 1993; Brodersen and Lindegaard 1999; van Hardenbroek et al. 2011). Also, Heiri (2004) found that sediment cores taken at any part of the basin in shallow Norwegian lakes included the dominant taxa, although with varying abundances.

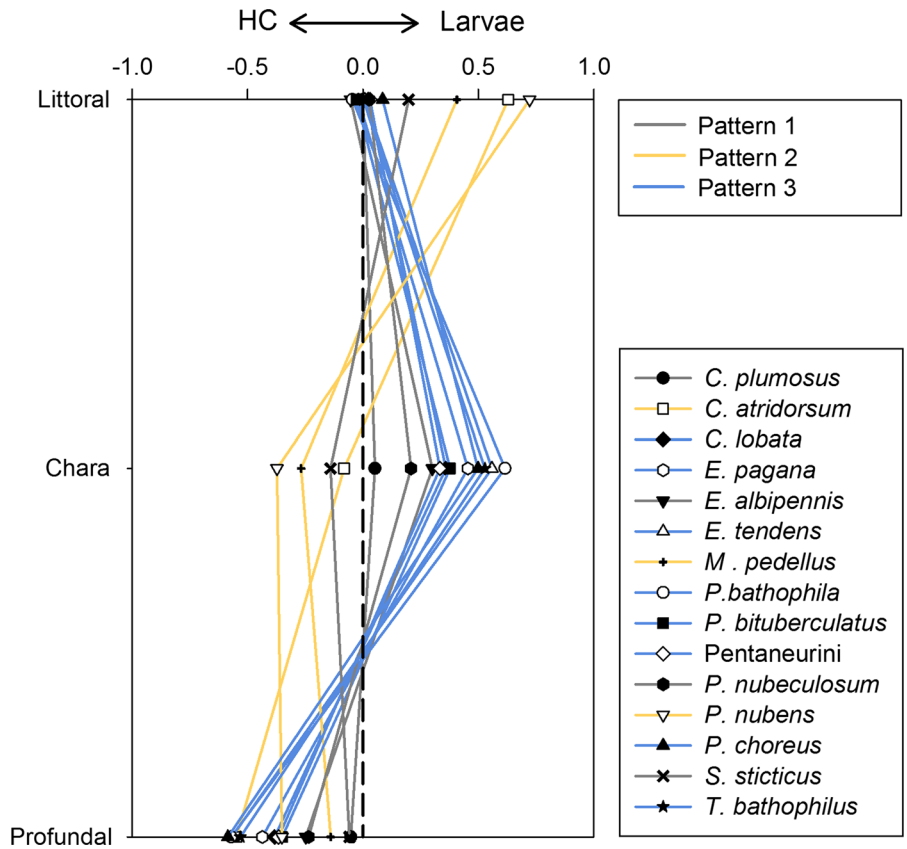

Fig. 5 'Transport Index' representing the overrepresentation of larvae or chironomid head capsules remains at every significant zone. The index compares the difference between the abundance of larvae and head capsules for each taxa at every depth category. Positive values of this index are related to an overrepresentation of larvae, whereas negative values are related to an overrepresentation of head capsules. Taxa labels follow the living assemblage nomenclature. (Color figure online)

Thus, our results suggest that a core retrieved at any depth except the littoral zone (0–2 m) and at 10–12 m could properly represent the living assemblage.

However, it is very important to notice that the lack of changes in the subfossil assemblage along the depth transect was largely driven by the dominance of a single taxon: *Paratanytarsus*. It was by far the most abundant taxon in the subfossil assemblages, both in terms of relative abundance (overall relative abundance = 45%, Table 1) and densities (more than 2 times higher than the second most abundant taxon). This was also the case for the living community of Enol Lake, as *Paratanytarsus* also reported the highest densities among chironomid larvae, which may explain the good correlation between the living overall community and the recent subfossil community. Moreover, this taxon was strongly associated with the *Chara* zone in the living community. This is in agreement with the habitat preferences of *Paratanytarsus* larvae, which are known to live preferentially in aquatic vegetation (Brodersen et al. 2001; Boggero et al. 2006). Thus, the dominance of *Paratanytarsus* head capsules along depth transect was most likely related with the presence of Characeae in the lake. The high productivity in terms of chironomid individuals related to this habitat, and the great dominance and densities of *Paratanytarsus* in the *Chara* zone, resulted in the homogenization of the recent subfossil assemblage along the depth transect. Other factors could be enhancing the transport of *Paratanytarsus* remains. For example, we observed tubes built by *Paratanytarsus* on *Chara* branches when processing living larvae samples. This tube-building behaviour could facilitate the dispersion and transport of their remains, since a large proportion of head capsules were not initially buried in the sediment but hanging from the branches of the aquatic macrophytes.

As it was reported in a previous study (Tarrats et al. 2017), *Chara* in Enol Lake, both in terms of abundance and composition. The importance of macrophytes presence and abundance is one of the main factors currently shaping chironomid assemblages as a driver of the subfossil assemblage has been already reported in several studies (Langdon et al.

2010; Luoto 2010; Rumes 2010; van Hardenbroek et al. 2011). Among macrophytes, *Chara* has been shown to be specially relevant for living (Hargeby et al. 1994; van den Berg et al. 1997, 1998; Cañedo-Argüelles and Rieradevall 2011) and subfossil chironomid communities (Brodersen et al. 2001; Ruiz et al. 2006). Thus, although in our study the recent subfossil assemblages offered a good representation of one of the main drivers of Chironomidae assemblages operating at the lake scale (i.e. the presence of *Chara*), other environmental factors that are currently affecting chironomids (e.g. anoxic conditions in deeper layers, temperature fluctuations in the littoral zone; Tarrats et al. 2017) are masked. This circumstance points out the major effect that a single factor can play on the subfossil chironomid community, and may hinder the use of these results to reconstruct past changes in other parameters rather than the presence of *Chara* (e.g. temperature, lake level). Our results suggest that using the recent subfossil community to build a transfer function could be misleading, since the environmental preferences of *Paratanytarsus* would have a great weight and the preferences of other taxa would be underrepresented. Moreover, since the presence and abundance of Characeae have been widely reported to fluctuate along time (Jeppesen et al. 1998; Rip et al. 2007; Scheffer and Jeppesen 2007; van Nes et al. 2007), recent subfossil assemblages may be excessively affected by a temporal and unstable situation. The existence of secondary gradients within the dataset that can act as confounding factors has been already described in previous studies (Langdon et al. 2010; Velle et al. 2010; Medeiros et al. 2015) and warns against the use of recent subfossil data without further questioning, as they could be greatly affected by several factors that could bias both quantitative and qualitative environmental reconstructions.

Although the overall subfossil assemblage was homogeneous, each taxon had different deposition patterns, as Figs. 4 and 5 show. Some taxa showed a lower transport range (i.e. living and subfossil abundances were very similar at a given depth) but others had a higher transport to other lake zones. As it was expected, the littoral zone was overrepresented by living larvae compared to the subfossil HC. This fact can be explained by a higher transport affecting littoral chironomids to deeper parts of the lake and can also explain the lower correlation levels reported at 2 m (Fig. 3a). The heterogeneous patterns reported in the *Chara* zone (Fig. 5) are related to the deposition of littoral taxa at these depths and the high productivity of certain *Chara*-related taxa, which are transported and deposited to deeper levels. At the same time, the low diversity in terms of chironomid living larvae caused an overrepresentation of the subfossil chironomids that are transported to the deepest areas. These heterogeneous patterns suggest certain complexity regarding chironomid HC deposition and transport, which was masked by the great dominance of *Paratanytarsus* in the overall community.

Conclusions

We found a great spatial homogeneity of the subfossil assemblage and a relatively strong correlation between the overall living assemblage (i.e. mean abundances of taxa) and the subfossil assemblage both in terms of taxa composition and abundance. Thus, according to our results, a single core taken at any depth would properly represent the whole living community of Enol Lake, except for depth intervals at which strong habitat differences exist (e.g. 0–2 and 10–12 m). However, the homogeneity of the subfossil assemblage along the depth transect did not match with the wide variety of habitat preferences of the living assemblage and was mainly explained by the great presence of *Chara*, which seems to promote the dominance of *Paratanytarsus* along the depth transect. Thus, caution should be applied when inferring past environmental conditions using the recent subfossil assemblage, at least in *Chara*-dominated lakes like Enol Lake. Overall, the results found in this study point out the potential confounding effect of a single factor in paleolimnological studies using chironomids. In this regard, we strongly recommend including studies aiming at understanding head capsules transport and deposition patterns before using subfossil remains to infer past environmental conditions, especially in deep lakes.

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