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RESEARCH ARTICLE

Comparing effects of microplastic exposure, FPOM resource quality, and consumer density on the response of a freshwater particle feeder and associated ecosystem processes

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Abstract

Fine particulate organic matter (FPOM) is an important basal resource in stream ecosystems for deposit- and filter-feeding macroinvertebrates (collectively 'particle feeders'). Microplastics (MP) share many characteristics with FPOM (e.g. size range, surface area to volume ratios) and are potentially consumed by particle feeders. Accordingly, MP contamination of natural FPOM pools might affect particle feeder growth and survival, particularly when background FPOM resource quality is low, or intraspecific competition is high. We conducted a microcosm experiment to evaluate how a realistic (1400 particles/kg sediment) polyethylene MP ($\phi = 45$–53 µm) concentration interacts with FPOM ($\phi = 63$–250 µm) resource quality (low versus high nutrient content) and consumer density (10 versus 20 individuals per microcosm) to affect growth and survival of larval *Chironomus riparius* (Diptera: Chironomidae), a model particle feeder. We additionally quantified community respiration, based on three hour measurements of oxygen consumption in the microcosms at the end of the experiment. MP exposure reduced larval body lengths by 26.7%, but only under the low consumer density treatment. MPs reduced community respiration by 26.2%, but only in the absence of chironomids, indicating an impact on microbial respiration. In comparison, low resource quality and high consumer density were associated with 53.5–70.2% reductions in community respiration, chironomid body length and/or body mass. These results suggest that effects of contamination of FPOM with MPs at environmentally realistic concentrations on the life histories of particle feeders such as *C. riparius* might be limited, especially relative to the effects of resource quality and consumer density. However, the reduction in microbial respiration when MPs were present highlights the need for further research addressing MP impacts on microbes, given their key roles in ecosystem functioning.

Keywords Fine particulate organic matter · Microplastics · *Chironomus riparius* · Consumer density · Resource quality · Community respiration

Introduction

Stream and river networks produce and transport tonnes of fine particulate organic matter (FPOM) [particle $\phi > 45$ µm, < 1000 µm (Hutchens et al. 2017)] every day (Malmqvist et al. 2001). FPOM particles include faecal particles (Shepard and Minshall 1984), other particulate detritus (Cummins and Klug 1979) and organic colloid flocculates (Wotton 2007). FPOM is a major component of nutrient and energy cycling in streams. FPOM provides a substrate for microbial biofilm formation, and constitutes a primary resource for deposit and filter feeding invertebrates, collectively termed 'particle feeders' (Fisher 1977; Malmqvist et al. 2001). However, stocks of FPOM in streams and rivers

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are increasingly contaminated by pollution from microplastic (MP) particles (Alimi et al. 2018), with a size range of 1–5000 µm (Frias and Nash 2019). Vast quantities of plastic waste enter aquatic ecosystems via terrestrial runoff (e.g. storm water from urban and industrial areas where plastic use is high), wastewater or wind (Zeng 2018). Some of this waste comprises primary MPs, directly released into the environment as spheres, irregular shapes (Gregory 1996) or fibres (Henry et al. 2019). In contrast, secondary MPs are generated from larger plastic waste through biotic-, e.g. microbial or animal activity (Immerschitt and Martens 2020), and abiotic degradation processes, e.g. UV photo-degradation (Barnes et al. 2009). FPOM and MP particles have overlapping size ranges (Webster and Meyer 1997; Thomas et al. 2001; Frias and Nash 2019) and densities (EPA 1992; Thomas et al. 2001), contain bioavailable organic carbon (Romera-Castillo et al. 2018) and host surficial biofilms (Zettler et al. 2013; Hossain et al. 2019; Chen et al. 2020). Consequently, contamination of lotic FPOM pools with MPs has potential to affect both the microbes and invertebrate particle feeders that regulate the cycling of FPOM in freshwater catchments.

Key particle feeding organisms in lotic ecosystems include larval Chironomidae (Diptera), especially the non-predacious species from the subfamilies Orthocladinae and Chironominae. These chironomids not only consume benthic FPOM, but also incorporate FPOM into construction of silken tubes within which they live (Mckie 2004; Goedkoop et al. 2007; Hölker et al. 2015). The deposit feeding and tube construction activities of chironomids in turn alter microhabitat structures and sediment microbial communities (Yeager et al. 2001). Larval chironomids contribute to bioturbation as individuals pump water through their tubes (Svensson 1997). Bioturbation and the potential for associated increases in bacterial production (van de Bund et al. 1994) together enhance the community respiration of microbes associated with detritus and sediments (Nogaro et al. 2008; Baranov et al. 2016) and support denitrification (Svensson 1998). These microbe-consumer interactions may be disrupted by MPs, directly affecting the survival and activity of chironomids and/or microorganisms (Huang et al. 2021). MPs might also be incorporated into chironomid tubes, as observed previously for Trichoptera larvae (Ehlers et al. 2019), potentially altering the functioning of these structures (Ehlers et al. 2020).

MPs have been shown to cause a range of effects on benthic particle-feeding organisms in aquatic ecosystems (de Sá et al. 2018). For example, Stanković et al. (2020) found that MP exposure slowed development time and increased final body size in the chironomid *Chironomus riparius*. Other recorded effects include reduced feeding of the marine lugworm *Arenicola marina* (Besseling et al. 2013) and reduced growth rates in the amphipod *Hyalella azteca* (Au et al. 2015). Such effects are likely to be at least partly attributable to a 'food dilution effect' (Ogonowski et al. 2018). Food dilution effects occur when a more labile food resource is mixed with a highly refractory substance that reduces nutrient concentration in the resource pool and increases food handling time (Ogonowski et al. 2016; Welden and Cowie 2016). Besides that, MP exposure can also affect metabolism and other physiological functions (Kratina et al. 2019), which over time might accumulate to impact consumer growth and survival, and ecosystem functioning (Prinz and Korez 2020). Despite the potential vulnerability of freshwater FPOM-based food webs to MP exposure, only one previous study has specifically investigated the impacts of MPs on ecosystem processes associated with FPOM particle feeders. Huang et al. (2021) focussed on processes of nitrogen removal mediated by microbes and *Chironomus riparius*. They found that although MP exposure promoted growth and activity of denitrifying microbes, the role *C. riparius* in mediating nitrogen removal was reduced, possibly due to a negative impact on its bioturbating activities.

Negative impacts of MP exposure arising from food dilution or physiological effects are likely to be stronger in consumer populations already experiencing limitations in resource quantity and/or quality (which collectively regulate resource availability to consumers) (McNamara and Buchanan 2005; Ieromina et al. 2014). The nutrient quality of FPOM is notably low in comparison with other aquatic resources (e.g. algae) (Callisto and Graça 2013; Bundschuh and McKie 2016), but is normally enhanced through the growth of surficial biofilms on particles (Cummins and Klug 1979; Joyce et al. 2007). In turn, surficial biofilm growth is strongly regulated by substrate characteristics [e.g. refractory carbon (C) content, C to nutrient ratios]. Accordingly, MP exposure that disrupts microbial activities and further dilutes the quality of an already low quality FPOM resource might have particularly strong potential to impact particle feeders (Miao et al. 2019a). Consumer density is a further key factor regulating resource availability. As consumer density increases, resource limitation is intensified as a consequence of competition (McKie et al. 2008). This may lead to negative density dependent effects on individual behaviour, growth and survival (Hooper et al. 2003), and on associated ecosystem processes (Klemmer et al. 2012). Both intra- and interspecific competition (i.e. competition within and between species, respectively) increases the vulnerability of organisms to additional stressors, e.g. exposure to pesticides, nutrients and low pH (McKie et al. 2009; Op de Beeck et al. 2018). However, the potential for additional environmental drivers, such as consumer density and resource quality, to regulate the impacts of MP exposure on consumers and associated ecosystem processes remains little assessed, especially in freshwater habitats.

This represents a knowledge gap that limits our capacity for assessing the potential impacts of MPs in freshwater ecosystems, relative to those of other key environmental drivers.

Here, we conducted a laboratory microcosm experiment to compare the effects of FPOM resource quality (low or high quality) and consumer density (0, 10 or 20 chironomid individuals per microcosm) with those of microplastic exposure on the growth and survival of *C. riparius* as a model particle feeder, and also on community respiration (i.e. bulk respiration of all organisms in the microcosms, including microbes and chironomids) as an ecosystem process. Our microplastic consisted of polyethylene (PE) particles, among the most dominant polymer types detected in environmental samples (Shim et al. 2018; Koelmans et al. 2019). The PE was in the form of primary MP bead particles, widely used in personal care products and thus readily entering freshwater habitats via wastewater. FPOM and spherical PE MPs were conditioned in stream water to grow surficial biofilm before the addition of chironomids. We expected that the survival of chironomid larvae would be reduced when reared at high density, reflecting the negative density-dependent effects of intraspecific-competition, and on the lower quality FPOM resource. We further hypothesised that these impacts would be strongest in microcosms contaminated by MPs due to the additional stress imposed by contamination of the consumers' FPOM food resource (i.e. in line with a food dilution effect). Finally, we hypothesised that community respiration would be greatest at the highest chironomid density and on the high quality FPOM resource, but would be reduced by the presence of MPs due to negative effects of MP exposure on chironomid biomass accrual and/or disruptions in the activity of microbial biofilms.

Methods

Experimental design

The study was conducted in a controlled environment room set at 20 ± 3 °C on a 16:8 h light–dark cycle. Glass crystallisation dishes (300 mL) were used as microcosms, each containing 80 g of sterile sand (Fontainebleau Sand, VWR). The experiment employed a full factorial design with three variables: FPOM resource quality (two levels: low quality, field-derived FPOM and high quality, laboratory-produced FPOM), chironomid consumer density (three levels: absence, 10 individuals or 20 individuals per microcosm) and MP presence (two levels: presence or absence of MPs). Each treatment was replicated five times leading to 60 microcosms across five randomised blocks.

Treatments

FPOM resource quality – two FPOM resource types were used in the experiment: the first was low quality, naturally occuring FPOM sourced from a forest stream, and the second consisted of a high quality heterogeneous lab mixture. The low quality FPOM resource was collected from depositional habitats in Fibyån Stream (59.884 N, 17.354 E), which flows through the Fiby Old Forest Nature Reserve (Ålandsdal, Sweden). We collected FPOM by carefully siphoning the top layer of the sediment using a 50 mL syringe. The collected material was filtered through nested sieves (250 µm and 63 µm) to remove any large debris and invertebrates. The FPOM material retained in the 63 µm sieve was then dried in an oven at 60 °C for 48 h and stored in glass jars. The high quality FPOM was prepared by combining ground Tetra Phyll fish food (Tetra, Germany) together with ground alder and birch leaves in a ratio of 1:1:2. The leaves were collected freshly abscised during autumn 2017 from one small alder and one small birch forest stand near Uppsala, Sweden that were not subject to anthropogenic fertilization. The high quality FPOM was passed through the same sieve set as used for the low quality FPOM, to ensure a comparable size distribution of particles. The carbon and nitrogen content of these FPOM resources were analysed at the UC Davis Stable Isotope Facility with an PDZ-Europe ANCA-GSL elemental analyser (SERCON Ltd, Cheshire, UK) interfaced to a continuous flow isotope ratio mass spectrometer (UC Davis 2020). The high and low quality FPOM resources had an average C:N ratio of 16.2 ± 0.0 and 47.5 ± 0.4, respectively. It is possible that the source materials used in both the low and high quality FPOM treatments were contaminated with some level of MP pollution. However, given we collected alder and birch leaf litter and natural FPOM from single locations, and used a single commercial preparation of fish food, we did not anticipate substantial variation in the level of such contamination, and expected that any such contamination was evenly distributed among our replicates.

Consumer density – the density of chironomids was varied by adding either 0, 10 or 20 newly hatched larvae (< 24 h old) into each microcosm dish. Five chironomid egg masses were obtained from a laboratory culture maintained at the department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, and hatched in a petri dish with the same water and temperature as the source culture (20 °C). Hatched larvae were gently mixed to facilitate random allocation of individuals from the five clutches among the microcosms. Once added to the microcosms, chironomid individuals settled on the bottom substrate and constructed tubes predominantly composed of the FPOM resource provided. In a pilot study, a consumer density of 10 allowed all individuals to construct robust, well-spaced tubes incorporating abundant FPOM particles (personal

observation, Supplementary Information, Fig. S1a). The doubling of density in the 20 individual treatments was thus presumed to increase competition for FPOM, and resulted in less well-spaced tubes incorporating lower quantities of FPOM per tube (personal observation; Supplementary Information, Fig. S1b). The densities used in this experiment (10 and 20 corresponding to 1411 and 2822 individuals m^{-2}, respectively) are within the range of densities (157 and 3384 individuals m^{-2}, mean 954 individuals m^{-2}) observed previously for northern European lakes (Mousavi 2002).

Microplastics – clear virgin polyethylene microspheres (Cospheric, 45–53 µm) were used in the MP treatment, at a concentration equivalent to 1400 MPs per $kg_{sediment}$ (0.669 mg per $kg_{sediment}$) or 747 MPs per litre of water (0.357 mg per L_{water}). The concentration used here is within the range of globally observed environmental sediment MP concentrations in some urban sites (Yang et al. 2021). We prepared a MP stock suspension of 0.01 g per L of de-ionised water. Unintended MP inputs were minimised by using glassware in the laboratory, with all containers pre-rinsed with 95% ethanol. Personnel always wore cotton clothing in the laboratory, and leaf litter was collected by hand and stored in cardboard boxes. When producing FPOM, we used a grinder with a stainless steel burr. Additionally, the stream water used in the microcosms were filtered through a stainless steel 25 µm sieve to remove any MPs above that size before the MP treatment was applied.

Addition of FPOM and MPs to the microcosms

Suspensions of FPOM resource (low or high quality) were prepared and added into each microcosm separately with 0.11 g of FPOM resource in 50 mL of de-ionised water. This amount of high quality FPOM resource was found in a pilot test to be sufficient for chironomids at a consumer density of 10 to reach pupation within 15 d. For microcosms exposed to MPs, we pipetted 5.35 mL of the MP stock solution into each MP treatment microcosm to achieve the desired concentration. The stock was sonicated for 5 s before each application to help evenly distribute particles. We confirmed realisation of the target concentration and effectiveness of sonication by visual enumeration of MP particles in stock samples under a light microscope (Supplementary Information, Fig. S2). All microcosms were then filled with 150 mL filtered stream water. The FPOM resource and MPs were conditioned in the microcosms for 7 d (after McKie et al. 2008) before chironomids were added. During this period, all microcosms were refilled every two days with approximately 25 mL filtered stream water to supplement the initial microbial colonisation, and to maintain both water depth (2 cm) and water nutrient concentrations close to that of the source stream. After the conditioning period, chironomids were added, with de-ionised water used for subsequent water level maintenance to minimise addition of dissolved minerals and colonisation by additional microbes. These experimental conditions were maintained for 14 days before the final measurements were made.

Data collection

At the end of the experiment, community respiration (i.e. bulk respiration of all organisms in a microcosm) was quantified in sets of eight microcosms (henceforth referred to as 'assay batch') using the dark–light bottle method of Johnson et al. (2009), as modified by Truchy et al. (2020). Briefly, each microcosm was filled with oxygen-saturated de-ionised water and the dissolved oxygen (DO) concentration measured using calibrated optical sensors (Firesting O_2 Meter, PyroScience, Aachen, Germany). Where possible, microcosms were taken from the same experimental block for each assay batch. Four crystallisation dishes containing only de-ionised water were also included to measure background O_2 fluctuations in the microcosm dishes (i.e. 'blanks' with only de-ionised water and sterile sand). All dishes were then sealed with parafilm, with care taken to avoid trapped air bubbles, and incubated in the dark. After three hours, the microcosm dishes were carefully unsealed and DO concentrations measured again. Community respiration (CR) is calculated as the difference between the initial and final DO concentration, corrected for the volume of crystallisation dishes and incubation time (Supplementary Information, Eq. S1). This was further adjusted for background DO fluctuations measured in the blanks.

Following respiration measurements, chironomids were collected and survivorship assessed. The collected chironomids were left to empty their guts overnight in de-ionised water prior to quantification of biomass. After 24 h, the chironomids were sedated with carbonated water and photographed under 10 × magnification. The photographs were analysed using ImageJ (V1.53a, National Institutes of Health, Bethesda, USA) (Schneider et al. 2012) to obtain the individual body lengths of chironomids. The chironomids from each microcosm were then dried at 60 °C in an oven for 24 h before total biomass was weighed to the closest 0.001 mg on a microbalance. Per capita biomass was calculated for each microcosm by dividing total biomass with the number of survivors.

Data analysis

Data were analysed using linear mixed models (LMM) with consumer density, FPOM quality and MP treatments fitted as fully crossed fixed effects. Random effects varied according to the response variable. Experimental block was fitted as a random effect for mortality and per capita biomass, while body length data was analysed using microcosm identity

nested within experimental blocks as a random effect. For analysis of respiration data, assay batch was fitted as a random effect to account for background variation among batches. Across all microcosm respiration rates, more random variation was explained by assay batches than the original experimental blocks (33.3% versus 16.2%, respectively). The primary test of significance was derived from the LMMs, but we additionally included significance tests based on Tukey's post-hoc test in our figures, to aid in assessment of differences among groups. One replicate was excluded from all analyses due to an error in the initial allocation of the number of chironomid larvae to that microcosm. There were also three replicates with extremely low survivorship (≤ 15%, one with and two without MPs). However, exclusion of these replicates did not change the outcomes of our statistical tests (no change in which terms were significant), and so were retained in our analyses. All data analysis was carried out using RStudio V3.62 (R Core Team 2019). R packages used were *ggplot2* for graphical plotting (Wickham 2009), *lme4* to construct LMMs (Bates et al. 2015), *lmerTest* to derive *p*-values for the LMMs (Kuznetsova et al. 2017) and *emmeans* to perform Tukey tests on the models (Lenth 2019).

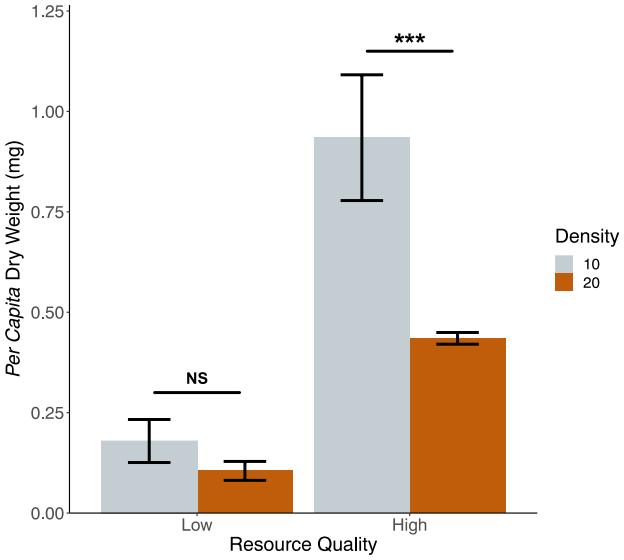

Fig. 1 Effects of FPOM resource quality and consumer densities on mean [± 1 standard error (SE)] per capita dry weight of chironomid larvae. Mixed model significance tests: density ($p < 0.001$), resource quality ($p < 0.001$), density × resource quality ($p < 0.010$). Tukey's post-hoc tests plotted on the graph. *NS* non-significant; $^{**}p < 0.010$, $^{***}p < 0.001$

Results

Chironomid survivorship, biomass and body length

Mean percentage survivorship was 66.7 ± 4.1%. Neither the three-way interaction between resource quality, consumer density and MP exposure (ANOVA, $F_{1, 27} = 3.25$, $p < 0.100$) (Supplementary Information, Fig. S3), nor any other interactions or main effects (all remaining $F \leq 1.1$, $p > 0.100$) (Supplementary Information, Table S1) were significant.

Chironomid mean per capita dry weight (g) was 473% higher for larvae fed the high (0.672 ± 0.093) compared with the low (0.142 ± 0.030 mg) quality FPOM resource ($F_{1, 27} = 52.2$, $p < 0.001$). Chironomid mean per capita dry weight was also 50% lower for larvae kept at the high (0.27 ± 0.04 mg) compared with low density (0.54 ± 0.12 mg) treatment ($F_{1, 27} = 15.0$, $p < 0.001$), pooling across the resource quality treatments. Additionally, there was a significant interaction between FPOM resource quality and consumer density ($F_{1, 27} = 8.38$, $p < 0.01$), with the negative effect of increased density on per capita dry weight more pronounced for individuals reared on the high quality FPOM resource (Fig. 1).

The individual body lengths of chironomid larvae were 245% higher when fed the high quality FPOM (10.3 ± 0.1 mm) compared with the low quality FPOM (4.2 ± 0.08 mm) resource ($F_{1, 15} = 236$, $p < 0.001$). Additionally, there was a significant interaction between consumer density and MP presence (ANOVA, $F_{1, 15} = 6.30$, $p < 0.05$). Individual body length was significantly lower for chironomids exposed to MPs under the low, but not high, density treatment (Fig. 2).

Community respiration

Community respiration was significantly affected by FPOM resource quality (ANOVA, $F_{1, 27} = 175$, $p < 0.001$). Respiration was 374% higher in microcosms with the high (4.41 ± 0.27 µmol O_2 hr^{-1}) compared with low (1.18 ± 0.09 µmol O_2 hr^{-1}) quality FPOM resource. There was also a significant interaction between consumer density and MP presence (ANOVA, $F_{2, 24} = 4.46$, $p < 0.050$), with respiration reduced only when MPs were present in the chironomid-free microcosms (Fig. 3). This interaction was further explored by analysing data for microcosms without chironomids alone, in which respirations is primarily attributable to microbial organisms. In these microcosms, respiration was 335% greater in replicates with the high (4.39 ± 0.44 µmol O_2 hr^{-1}) compared with low (1.31 ± 0.16 µmol O_2 hr−1) quality FPOM (ANOVA, $F_{1, 11} = 75.6$, $p < 0.001$). MP presence had a significantly negative effect on community respiration (ANOVA, $F_{1, 12} = 6.91$, $p < 0.050$; Fig. 4). A further interaction between FPOM resource and MP presence was non-significant (ANOVA, $F_{1, 15} = 3.86$, $p > 0.050$), with a trend for lower community respiration in the presence of MPs when

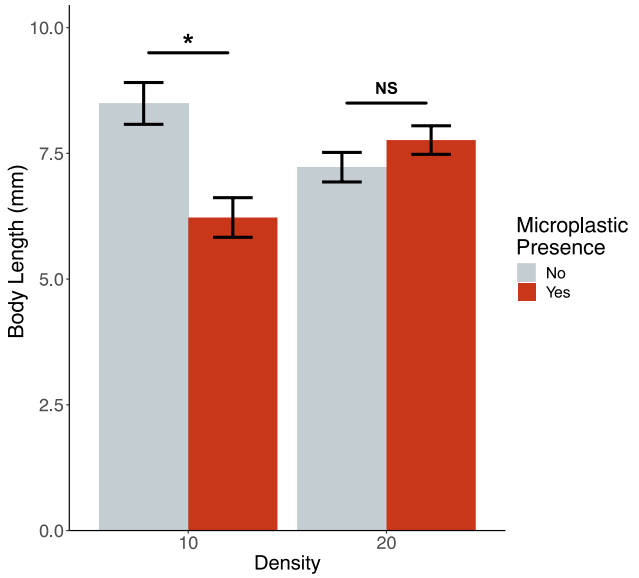

Fig. 2 Effects of consumer densities and microplastic exposure on mean (± 1 SE) chironomid body length. Mixed model significance tests: density ($p < 0.100$), MP ($p < 0.100$), resource quality ($p < 0.001$), density x MP ($p < 0.050$). Tukey's post-hoc tests plotted on the graph. *NS* non-significant; ***$p < 0.001$; *$p < 0.050$

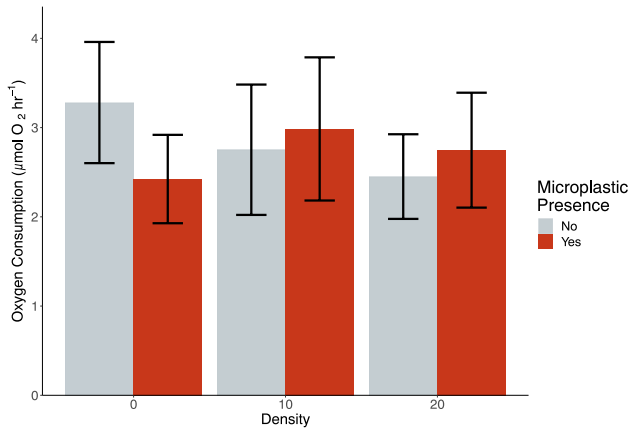

Fig. 3 Effects of consumer density and microplastic exposure on mean (±1 SE) community respiration of microcosms. Mixed model significance tests: density ($p > 0.050$), MP ($p > 0.050$), density × MP ($p < 0.050$). No Tukey's post-hoc test significance

provided with the high quality, but not the low quality, FPOM. In contrast, community respiration of microcosms with chironomids was significantly affected by FPOM resource quality only (ANOVA, $F_{1, 32} = 111$, $p < 0.001$) (Supplementary Information, Fig. S4), with rates 380% higher in microcosms with the high (4.22 ± 0.35 µmol O_2 hr^{-1}) compared with low (1.11 ± 0.11 µmol O_2 hr−1) quality FPOM resource.

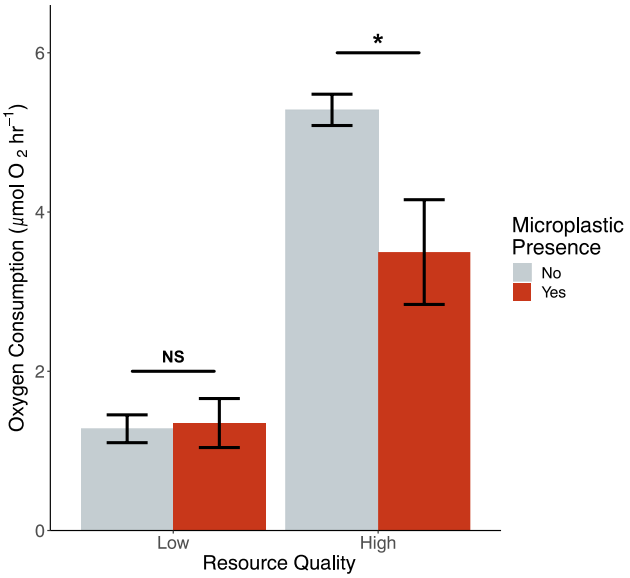

Fig. 4 Effects of FPOM resource quality and microplastic exposure on community respiration (±1 SE) of microcosms without chironomids. Mixed model significance tests: resource quality ($p < 0.001$), MP ($p < 0.050$), resource quality × MP ($p > 0.050$). Tukey's post-hoc tests plotted on the graph. *NS* non-significant; *$p < 0.050$

Discussion

In a microcosm experiment, we evaluated the effects of a realistic substrate concentration of polyethylene MP particles on the survival and growth of a model particle feeding chironomid and on community respiration, relative to those of additional environmental drivers. FPOM resource quality and consumer density were clearly the predominant drivers of both organism growth and community respiration. Nevertheless, there was evidence for contingent impacts of MP exposure on chironomid body length and community respiration. MP exposure reduced chironomid body length under the high, but not low, FPOM resource quality treatment. MP exposure also reduced community respiration, but only in the microcosms without chironomids present, indicating an impact on microbially-mediated community respiration. The effect sizes of these MP impacts were limited relative to the much stronger effects of consumer density and resource quality, similar to previous studies which demonstrated lower levels of impact from MPs relative to other stressors, such as temperature (Hiltunen et al. 2021) and pesticides (Horton et al. 2018).

Individual and population responses

We did not observe a systematic effect of either resource quality, consumer density or MP presence on survivorship of chironomids. High mortality in some individual replicates

was also not clearly associated with any of the experimental treatments or blocks, and is thus difficult to explain, but seems most likely to reflect random variation in the initial survivorship of the newly hatched larvae, which was not easily quantified owing to their extremely small size. Neither resource quality, consumer density nor MP exposure were predicted a priori to induce a strong acute mortality response. However, we did observe a systematic effect of resource quality on chironomid growth, which we hypothesise could compromise survivorship over a longer period than assessed here. Growth was very limited for larvae reared on low quality FPOM, with most individuals failing to develop beyond the second instar. This suggests the low quality FPOM resource was very limited in availability of key nutrients required for supporting growth and development, which are likely to affect survivorship in the longer term, and in particular the success of pupal metamorphosis (Wesner et al. 2020). Accordingly, a longer study period, including rearing the larvae to adulthood, might be necessary for detection of potential survivorship differences associated with the low resource quality treatment.

The limited development of larvae grown on the low quality FPOM resource was manifested in reduced individual body length and per capita biomass, relative to the high quality FPOM treatment. Notably, the C:N ratio of our low quality, field collected, FPOM (47.5) was higher than any previously reported value for naturally occurring FPOM in heterotrophic steam ecosystems (e.g. C:N ~ 10–35) (Cross et al. 2003; Callisto and Graça 2013; Yoshimura et al. 2008). In contrast, the C:N ratio of our high quality FPOM resource (16.2) is characteristic of the highest quality plant detritus in stream ecosystems, such as the nitrogen rich litter of *Alnus* (17.5–19.2) (García-Palacios et al. 2016), and was supplemented with additional nutrients from the commercially available fish food included in the mixture. The field-collected FPOM in our study was dried to facilitate mass determination, but was then reconditioned in stream water to re-establish surficial biofilms, which is an important factor in enriching the nutrient quality of particles in situ (Cummins and Klug 1979). We might not have achieved levels of conditioning in the laboratory comparable to what is typically seen in situ, which would then have further limited nutrient quality of the field collected FPOM. Nevertheless, these results indicate that a diet consisting of naturally occurring FPOM on its own has extremely limited capacity for supporting consumer growth. This is important in contextualizing potential MP impacts on heterotrophic freshwater ecosystems, given that naturally occurring FPOM pools are not themselves necessarily highly nutritious. For example, the potential for microplastic contamination of organic sediments to be associated with significant 'food dilution effects' on consumers is likely to be limited when the organic matter is itself extremely low quality (Ogonowski et al. 2018), as observed here.

Contrary to our hypothesis, there was no evidence that exposure of chironomid larvae to the greater potential stress associated with the low food quality or high consumer density increased the likelihood of negative impacts of MP contaminationthe opposite for per-capita growth. Rather, we observed the opposite for per-capita growth: MP exposure negatively impacted individual body lengths of chironomids reared at low consumer density. MP exposure has been associated with reduced growth in macroinvertebrates (Au et al. 2015; Redondo-Hasselerharm et al. 2018), likely due to dilution of dietary intake with MP particles characterised by minimal nutritional value, and possibly the increased metabolic costs to excrete these particles (Foley et al. 2018). Reduced growth of prey organisms due to MP exposure may lead to knock-on effects on predators as smaller prey organisms become more common. Our findings suggest that negative effects of MPs on growth are more likely to affect chironomids in lower density aggregations. We hypothesise that this surprising result might reflect the production of higher volumes of faecal particles in the higher density chironomid aggregations. Invertebrate faecal particles are colonised by bacteria which thrive in invertebrate digestive tracts, and contribute additional exudates and bacterial cell biomass compared with FPOM prior to gut passage, and might be primed for further conditioning upon egestion (Ward and Cummins 1979; Wotton and Malmqvist 2001). These rapidly conditioning and tightly packed particles might in turn reduce negative effects of MP exposure by increasing the pool of more nutritious FPOM. Alternatively, the lower level of competition at low consumer densities might have allowed individual larvae to spend more time in resource acquisition compared with inter-specific interactions, increasing their exposure to potential negative effects of MPs contaminating their food resource. Further research is required to assess these alternative explanations.

Community respiration and chironomids

Unexpectedly, there was no significant difference in community respiration between microcosms with and without chironomids, and consumer density did not affect respiration rates. These findings indicate that, overall, community respiration was dominated by microorganisms (Fisher and Likens 1973), without any evidence that chironomid bioturbation increased net respiration rates. Instead, community respiration was overwhelmingly driven by FPOM resource quality, with respiration rates substantially greater in microcosms with the high quality FPOM resource. The very low respiration rates observed on the low quality FPOM are in line with those observed for consumer growth, highlighting the limited capacity of the natural FPOM resource to support

metabolic activity compared with the more nutrient rich, high quality resource.

MP presence reduced community respiration, but only in microcosms without chironomids. This suggests that MP exposure reduces the respiration of microbes associated with the organic sediment and other substrates in our microcosms, but that this effect was obscured when chironomids were present. There was also a trend for a stronger negative effect ($p = 0.068$) of MP presence on microbially-mediated community respiration (in the absence of chironomids) in microcosms with the high quality FPOM resource, but more research is required to confirm this result. MPs have been shown to harbour distinct and often less diverse microbial assemblages compared with naturally occurring substrates (McCormick et al. 2014; Kettner et al. 2017; Miao et al. 2019b; Li et al. 2020). Changes in microbial community composition and diversity have been linked with altered ecosystem functioning in detrital food webs (Gardeström et al. 2016), and there is some evidence linking shifts in microbial communities associated with MP and nanoplastic exposure to changes in ecosystem functioning (Arias-Andres et al. 2018; Huang et al. 2021; Seena et al. 2022). It is similarly possible that the change in microbial respiration observed here reflects a change in microbial composition, activity and/or biomass.

Implications and conclusions: microplastic impacts in freshwater particle-processing chains

Our study is most relevant for benthic food webs in heterotrophic streams and rivers with nutrient-poor pools of FPOM and high levels of mineral sediment (as in our experimental microcosms). In these habitats, the overall resource quality of the particle pool is unlikely to be substantially impacted by the addition of MP particles. This contrasts with many previous studies of MP impacts on freshwater organisms, which have focussed on filter feeding pelagic organisms consuming algal and bacterial cells, and where ambient concentrations of mineral sediments and low quality FPOM are much lower than those our benthic deposit feeders are exposed to (Canniff and Hoang 2018; Aljaibachi et al. 2020). Our study focussed on one type of polymer (albeit one of the most abundant in most freshwater habitats) and presented only as spheres, which is relatively uncommon in the environment (Burns and Boxall 2018), and it is possible the impacts of the different shape and polymer combinations could differ from those observed here. Nevertheless, our results highlight the risk for MPs to affect consumer life histories and microbial processes in benthic habitats. In particular, the interaction observed between MP exposure and consumer density demonstrates the potential for MPs to interact with other environmental drivers, highlighting the need for a more thorough investigation of potential interactions between MP exposure and additional stressors.

In the Anthropocene, MP pollution is just one pressing environmental issue amongst the broad array of anthropogenic pressures currently impacting ecosystems. Up to now, the lack of research focussed on ecosystem-level impacts of MPs in freshwaters limits the possibility for scientific knowledge to inform priority setting in monitoring, policy and management of MP pollution, relative to other anthropogenic pressures. Our findings suggest that MPs, applied at an environmentally realistic concentration might have some impacts on the growth and survival of consumers and on microbial respiration in benthic stream FPOM-based food webs. Although the magnitude of these impacts were limited relative to the much stronger effects of resource quality and consumer density, we emphasise that we always used MP concentrations that spanned the range of currently observed real-world concentrations. It is thus possible that some of these effects will strengthen with projected increased MP concentrations in the future, in line with the amount of plastic debris already accumulated in freshwater habitats, which has yet to degrade to MP size. Furthermore, our evidence for an effect of MPs on microbial respiration in particular point to risks for knock-on effects on other organism groups and ecosystem properties, given the key role of microorganisms as not only a resource but also in mediating fundamental ecosystem processes, including nutrient and carbon cycling.

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Data availability Data collected and analysed are available from the authors upon reasonable request.

Declarations

Conflict of interest All authors declare no conflicts of interests.

Ethical approval No ethical approval was required for this study as experimental work was conducted with an unregulated invertebrate species (*Chironomus riparius*).

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