



Microplastics alter multiple biological processes of marine benthic fauna

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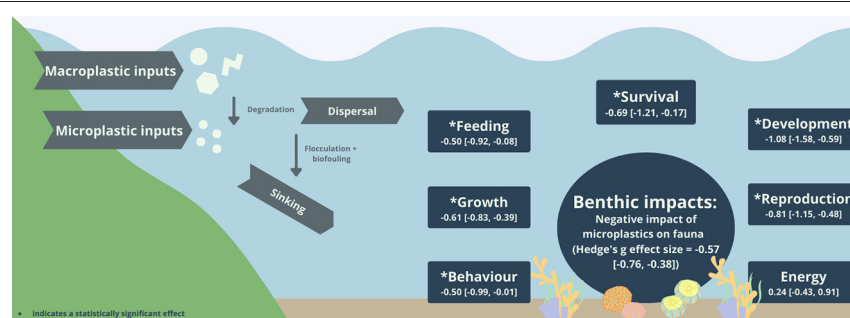
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HIGHLIGHTS

- Meta-analysis revealed microplastics weaken multiple processes fundamental to seabed life.
- Surge in research helps establish that plastic impacts are stronger than thought.
- Severity of impact depends on feeding strategy, life stage and taxonomic group.
- Early life stages are most strongly impacted by microplastic exposure.
- Leaking chemicals generate stronger responses than plastic particles themselves.

GRAPHICAL ABSTRACT



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ABSTRACT

Marine sediments are a sink for microplastics, making seabed organisms particularly exposed. We used meta-analysis to reveal general patterns in a surge in experimental studies and to test for microplastic impact on biological processes including invertebrate feeding, survival and energetics. Using Hedge's effect size (g), which assesses the mean response of organisms exposed to microplastics compared to control groups, we found negative impacts (significant negative g values) across all life stages (overall effect size (g) = -0.57 95% CI [-0.76 , -0.38]), with embryos most strongly affected (g = -1.47 [-2.21 , -0.74]). Six of seven biological process rates were negatively impacted by microplastic exposure, including development, reproduction, growth and feeding. Survival strongly decreased (g = -0.69 [-1.21 , -0.17]), likely due to cumulative effects on other processes such as feeding and growth. Among feeding habits, omnivores and deposit feeders were most negatively impacted (g = -0.93 [-1.69 , -0.16] and -0.92 [-1.53 , -0.31], respectively). The study incorporated the first meta-analysis to contrast the effects of leachates, virgin, aged and contaminated particles. Exposure to leachates had by far the strongest negative effects (g = -0.93 [-1.35 , -0.51]), showing studies of contaminants and leachates are critical to future research. Overall, our meta-analysis reveals stronger and more consistent negative impacts of microplastics on seabed invertebrates than recorded for other marine biota. Seabed invertebrates are numerous and diverse, and crucial to bottom-up processes, including nutrient remineralisation, benthic-pelagic coupling and energy transfer through the ocean food web. Marine sediments will store microplastics over long timescales. The reveal that microplastics impinge on multiple fundamental biological processes of seabed fauna implies plastic pollution could have significant and enduring effects on the functioning of the ocean.

1. Introduction

The problem of plastic pollution is growing, resulting from an average annual increase of 9% in plastic manufacturing between 1950 and 2009

(Hammer et al., 2012). The input of plastics into the marine environment, both directly and indirectly through riverine inputs, is also increasing. An estimated 4.7 to 12.8 million tonnes of plastic enters the marine environment every year (Agamuthu et al., 2019). The fate of much of this plastic is unknown; the term 'missing plastic' was coined to describe the shortfall in the estimated volume of plastics found in the water column compared to inputs (Wayman and Niemann, 2021). It is thought that deep-water

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and sediment storage of plastics and microplastics, in particular, make up the majority of this 'missing plastic' (Zhang, 2017). Here, we assess the impact of accruing microplastics on invertebrate animals of the seafloor.

The definition of microplastics is inconsistent throughout the existing literature, but most commonly includes plastic particles of any shape from 0.1 μm to 5 mm (Auta et al., 2017). Within this category exist intentionally manufactured primary microplastics, such as highly prevalent pre-production plastic 'nurdles' (Jiang et al., 2021), as well as secondary microplastics, resulting from the UV or physical degradation of marine macroplastics (Efimova et al., 2018). Microplastic prevalence in the ocean was recently estimated at 2.41 million tonnes across the Atlantic, Indian and Pacific subtropical gyres (Vazquez and Rahman, 2021). This prevalence is likely to increase with inputs not only from terrestrial activity, but also from the breakdown of plastics already present in the marine environment (Kooi et al., 2017). Microplastics are subject to further change upon entering the marine environment; they may be further broken down into nanoplastic particles (<0.1 μm) or experience biofouling (Zhang, 2017). Biofouling of microplastics occurs predominantly as a result of the attraction of organic substances to the hydrophobic surface of the particle (Kaiser et al., 2017). C  zar et al. (2014) showed that the specific density of most microplastics is lower than that of seawater, so particles should remain buoyant. However, settling of microplastics on the seafloor has been documented, with Zhang (2017) suggesting sinking rates of approximately 4 mm per day. Sinking is stimulated by the biofouling of microplastic particles which increases the specific density, although studies have also suggested the influence of microplastic shape and size on the sinking rate of a particle (Melkebeke et al., 2020). Using Environmental Risk Assessment modelling, Everaert et al. (2018) found species had varying sensitivity to microplastic, but that sediment concentrations <540 microplastic particles kg^{-1} were 'safe' and unlikely to have negative impact. The same study reported a current concentration of 32–144 particles kg^{-1} in marine intertidal sediments, suggesting that the safe threshold is likely to be exceeded in the latter half of the 21st century. Estimates of microplastics in seawater itself vary widely and Xu et al. (2020) reported seawater concentrations ranging from 0.33 to 3252 particles m^{-3} globally. The vast majority (>90 %) of marine microplastics have been reported to accumulate on the seafloor (Melkebeke et al., 2020). In the southern North Sea, for example, sediment microplastics have been reported to range in concentration from 2.8 to 1188.8 particles kg^{-1} dry weight (Lorenz et al., 2019). Microplastics are therefore likely to become a ubiquitous component of seabed sediments and thus the influence of microplastics on benthic habitats must be considered.

Gall and Thompson (2015) reported over 44,000 interactions of marine fauna with plastic debris, across 693 species. Larger plastic fragments impact fauna predominantly through ingestion and entanglement. A systematic review of 747 studies quantifying the interactions of plastics with marine megafauna found 701 species had ingested plastics and 354 species had experienced entanglement (K  hn and van Franeker, 2020). Microplastics can impact marine organisms through a wider range of mechanisms, as shown in many experimental laboratory studies. Microplastic exposure caused abnormal embryo development in the brown mussel *Perna perna* (Gandara E Silva et al., 2016). The lugworm *Arenicola marina* reduced its feeding rate with increasing microplastic dosage (Besseling et al., 2013). Reduced feeding can be the result of a false sense of fullness, damage or blockages to the digestive tract or confusing microplastics for prey (de S   et al., 2015). Numerous studies have found cellular level impacts of microplastics, for example, microplastic consumption influenced cellular pathway signalling, diminished growth and induced toxicity and oxidative stress in rotifers (Jeong et al., 2016). Such impacts may lead to behavioural changes, growth inhibition and, ultimately, increased mortality (de S   et al., 2018). Microplastics also have the potential to cause adverse reactions via persistent organic pollutants (POPs), which adhere to plastic particles. Particularly hazardous are endocrine disruptor chemicals (EDCs), which accumulate in fatty tissues, altering hormone production and potentially causing thyroid problems, reduced reproductive success and hormone-sensitive cancers (Gallo et al., 2018). While the study of

POPs so far has focussed primarily on the impacts on human health, effects on marine fauna have been observed, one example being reduced survival rate and jump height in beach hoppers (Tosetto et al., 2016). Microplastics encountered in nature are often contaminated, giving them the potential to be more toxic than virgin microplastics. Abnormal development was found in 23 % of brown mussel *Perna perna* embryos from virgin pellets compared to 100 % abnormal development from pellets sourced from beach sediments (Gandara E Silva et al., 2016). Despite such indications of impact to benthic organisms, there is no overview of implications to the breadth of seabed organisms. In a systematic review of 220 studies published prior to the year 2010, Ajith et al. (2020) found that 38 % of existing studies on the impacts of microplastics had used fish as the study organism, followed by 18 % studies targeting molluscs. This leaves a knowledge gap surrounding the majority of benthic invertebrate species. Here, we make use of a rapid increase in publications on marine benthos since 2019 (Fig. S2, Supplementary Materials) and new data for a total of 6 taxa to generate a comprehensive overview across seabed taxonomic and functional groups.

As a means of quantifying the impacts of microplastics on marine fauna, recent studies have considered the impact of microplastics on what was termed the 'functional traits' of organisms (Berlino et al., 2021; Salerno et al., 2021), albeit several 'traits' are more correctly perceived as the rates of important biological processes like growth, reproduction and survival (See Supplementary Materials, Table S1). Focussing on biological rates offers insights into the impacts of microplastics on wider organismal and ecosystem functioning. Since many impacts of microplastics result directly from the ingestion of particles, feeding strategy in particular may contribute to variation in the magnitude of impacts. Thus, among fish and invertebrates, predators and deposit feeders contained more plastics than filter feeders and, sometimes, deposit feeders (Bour et al., 2018; Naji et al., 2018). It stands to reason that if the ingestion of microplastics varies by feeding strategy, so might the effects on biological processes.

There is a lack of consensus of the impacts of microplastics on marine benthic fauna, particularly in terms of the range of factors which might be contributing to the variation in effects. Here, we make use of a rapid increase in publications on marine benthos since 2019 with new data for a total of 6 phyla to generate a comprehensive overview of the impacts of microplastics across seabed taxonomic and functional groups. Using a systematic review and associated meta-analysis of extracted data we quantify the impacts of microplastics on marine benthic fauna and identify knowledge gaps and potential bias in the current state of the art. We hypothesised that microplastics would have an overall negative effect on the performance of marine benthic fauna, which would increase with exposure concentration. We expected the effects of microplastics to vary among feeding habits, with predators at risk of stronger effects resulting from trophic transfer of microplastic particles. Microplastic characteristics, including size, shape, exposure duration and concentration, were expected to be primary drivers of any variation in effect size.

2. Materials and methods

2.1. Study design

The study used a systematic review and meta-analysis to assess the impacts of experimental exposure to microplastics particles (hereinafter, MPP will refer to microplastic particles) on marine benthic fauna. Only laboratory studies that included a control (no MPP) and one or more MPP exposure levels were included, so that overall mean effect sizes could be determined. Studies focusing on MPP ingestion but not impacts on biological processes were excluded. The review had no geographical or temporal limits. Two search engines, Web of Science and the Wiley online library, were used in order to include papers from a range of sources, including grey literature, and minimise publication bias otherwise arising from restricting search results to peer-reviewed journals favouring studies with significant results (Sterne et al., 2000). Ultimately, all studies included in

the analysis were from peer-reviewed journals. The study considered the influence of potential contributing factors, such as phylum, feeding strategy and microplastic composition, on variation in the magnitude of microplastic impacts (see Supplementary Materials, Fig. S1).

2.2. Literature search and data extraction

The systematic literature search was conducted on the 7th June 2021, following the methodology of Pullin and Stewart (2006) and O'Dea et al. (2021). The search string had three components using the Boolean operators “AND” and “OR”. Each component of the string was designed to address an area (impact, microplastics or biological processes) of the research question and to include studies on any marine benthic fauna. The string of search terms was tested to ensure it delivered relevant literature hits (tested using 10 pre-identified highly relevant key references. Table S2). The final string of search terms was as follows:

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impact* OR response* OR effect* OR interaction* OR consequence* OR implication* OR
contamination* OR ingestion* OR consumption* OR consume* OR uptake* OR "taken up"
OR accumulation OR contamination OR transfer
AND
Microplastic* OR "micro plastic" OR "micro-plastic" OR microfibrilament* OR filament* OR
"plastic pellet*" OR nurdle*
AND
trait* OR "functional trait*" OR growth OR feeding OR reproduction OR fecundity OR
behaviour* OR development OR hatching OR health OR survival OR digestion

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A total of 3650 search results (studies, papers) were identified on Web of Science, with a further 166 from the secondary Wiley Online Library. For each paper, the title, then abstract and then the full-text content were screened for relevance (Table S3) according to the following criteria. Studies that purely addressed the distribution or sources of microplastics were excluded, as were observational work documenting only the ingestion of microplastics, qualitative and systematic reviews. Changes to feeding rates following microplastic consumption were included, but ingestion rates of microplastic particles themselves were not included as a change to a biological process. Experimental studies with a focus on cellular impacts were also excluded, unless the impact could be tied directly to one of the biological processes we evaluated (e.g. O₂ consumption, representing respiration and energy demand). Only studies focussing on marine benthic organisms were considered. Freshwater organisms or those from inland saltwater were excluded, while both intertidal and subtidal marine and estuarine organisms were included, where the species was determined to spend the majority of its lifecycle on, or buried within, the seafloor. Experiments which used microplastics of sizes outside of the predetermined range (0.1 µm–5 mm) were excluded. A final list of 72 papers (Table S3) was selected for meta-analysis.

Data were extracted directly from paper text, tables and figures, the latter using Automeris WebPlotDigitizer Version 4.4. Types of data extracted from each study were study identifiers, meta-data and data for quantitative synthesis (control and experimental mean, standard deviation, SD, and number of replicates, n) (Table S4). Examples of response variables which were used for biological traits are outlined in Table S1. A total of 701 case studies (independent experiments included in the same study. For example, multiple exposure concentrations or species tested) were extracted from the 72 papers.

2.3. Data analysis

Data extracted from papers required standardisation before analysis to overcome the use of different units and approaches among studies. The data were standardised to common units of microplastic exposure

concentration, duration and particle size in order to allow comparison of the experimental conditions that test animals were exposed to. Microplastic particles were classified into: fibre, fluff (usually derived from clothing fibres), fragment, pellet, square, sphere (including microbeads) or powder, plus leachates and leachates adsorbed to microplastics, according to how they were described by the authors (see e.g. Gray and Weinstein, 2017). Microplastic exposure units which could not be standardised into common units (e.g. % sediment weight, fibres per prey individual) were excluded from concentration analysis (18 studies). Remaining microplastic exposure units from 54 studies were standardised into common units of g L⁻¹. Concentrations given in particles L⁻¹ were converted using $\text{mass}_{\text{particle}} = \text{density} \times \text{volume}$ (Everaert et al., 2018), using a standard density of marine microplastics of 0.925 g cm⁻³, determined by Van Cauwenberghe (2016). Density of plastic particles was not available for the microplastics used in most studies and using this standard density was the most appropriate approach. Particle volumes were calculated for spheres (and for fragments, with assumptions of largely spherical shape) using $V = 4/3\pi r^3$, where the radius of the particle was provided in the original study. Microplastic concentration was log transformed for analysis to allow patterns to be more clearly seen, since data were skewed towards very small values. Where necessary, medians and interquartile ranges (IQR) were converted into means and standard deviations (SD), where SD was taken to equal IQR/1.35, assuming normal distribution of data (Higgins et al., 2019). Any 95 % confidence intervals (CI) were also converted into SD, where $\text{SD} = \text{CI}/3.92$, multiplied by the square root of the sample size (n) (Higgins et al., 2019). Data were explored for patterns in the number of studies per geographical region, taxa (phylum of organism), feeding strategy (predator, deposit feeder, scavenger, filter feeder, omnivore) and microplastic characteristic (shape, size, polymer type) to generate an overview of the geographical distribution of research and to identify potential bias within the results, such as a high proportion of studies published in one geographic region.

Effect size for each study was calculated as Hedge's *g* (Borenstein et al., 2009):

$$\text{Hedge's } g = \frac{m_c - m_e}{SD_{\text{pooled}}} \times J$$

where m_c was the control mean, m_e was the experimental mean, SD_{pooled} was the pooled standard deviation across the samples and J was the correction factor used to account for bias arising from variation in sample size.

Hedge's *g* values were interpreted using the recommended thresholds from Cohen (2013), where ~0.2 indicated a small effect, ~0.5 indicated a moderate effect and >0.8 indicated a larger effect. A negative Hedge's *g* represents a negative impact of the experimental condition relative to the mean. Directionality of effect sizes was corrected to ensure *g* values were representative of the effects shown by studies and as described by the authors (Table S5). For example, an increased time to find a new shell (automatically a positive effect) was corrected to be negative, when the authors noted this represented a negative impact on the organism (Crump et al., 2020). We checked for any influence of publication bias by applying the non-parametric trim and fill method (Duval and Tweedie, 2000) to an rma.uni model of our data, whereby the number of missing studies at either extreme positive or negative values could be estimated. This showed that publication bias was likely to have had a negligible effect on the outcome of our meta-analysis (Table S6).

Once an effect size had been determined for each case study ($k = 701$, where k signifies independent experiments, or case studies, included in the same study), a pooled effect size was calculated for all values and each biological process, using a random effects model with the “rma.mv” function of the “metafor” package (Viechtbauer, 2010) in Rstudio Version 1.3.1093 (RStudio Team, 2020). In each model, we included ‘Study ID’ of the published study to account for non-independence of data extracted from the same study (Viechtbauer, 2007). To evaluate data compliance with test assumptions, an I² value was produced by Wald's test for heterogeneity of variance between studies (Borenstein et al., 2009) and a Cochran's Q value

determined the level and significance of heterogeneity (Cochran, 1954). Since results from the random effects model indicated significant heterogeneity between studies, subgroup analyses (categorical data) and meta-regressions (continuous data) were conducted using random effects models in metafor (R statistics) to identify moderator variables which may have been driving the variation. Organism traits such as taxa, feeding type and life stage and experimental variables including microplastic size, shape, polymer type and concentration, were investigated for contribution to heterogeneity as well as the pooled effect size for each variable. Effect sizes were given with 95 % confidence intervals.

3. Results

3.1. Summary and distribution of findings

While no temporal limits of publication were implemented, all papers were published from 2013 onwards, with 79.2 % published since 2018 and nearly half (43.1 %) published in the last 1.5 years covered by our systematic review (Fig. S2). Published findings were from 6 continents, leaving only Antarctica absent, with the most research having occurred in Europe ($n = 35$) and Asia ($n = 17$) (Fig. S3).

Experiments involved 6 animal phyla and 6 feeding strategies (Fig. 1), with the majority of studies focused on filter feeders ($n = 39$). A wide range of experimental conditions were used by studies. Exposure concentrations were reported in a multitude of units, of which ' g L^{-1} ' and ' particles L^{-1} ' were the most common, with less frequently used units including '% of feed' and '% of sediment weight'. Approaches to reporting microplastic leachates were varied, since some studies used leachates adsorbed to particles and others used leachates independently (reported as concentration in the water column). The majority of studies ($n = 26$) exposed organisms to microplastic spheres, although 30 studies did not state the shape of particles. Out of 19 types and combinations of polymers used for exposure, polystyrene and polyethylene were the most commonly used ($n = 25$ and $n = 10$, respectively).

3.2. Effects of microplastics on biological processes

The effect size for all organisms pooled indicated a moderate, but significant overall negative effect of microplastics on biological processes ($g = -0.57 [-0.76, -0.38]$, $p < 0.001$) (Fig. 2). Significant negative effects were also seen for all categories of biological processes, except energy use (e.g. respiration). Large negative effects of microplastic particles (MPP) on animal development, reproduction and survival were seen (Fig. 2). A small and non-significant effect of MPP on energy processes was found. Significant heterogeneity of variance was found between studies ($I^2 = 61.4\%$, $Q_{700} = 2668.9$, $p < 0.001$), including within every biological process category (Table 1), indicating unexplained variance beyond the effect of biological process and supporting the need for a sub-group analysis to investigate other drivers of effect size.

3.3. Sub-group analysis

3.3.1. Organism characteristics

The taxonomic group of organisms explained a significant amount of heterogeneity of variance in the dataset ($Q_{\text{moderators}, 6} = 39.87$, $p < 0.001$). Microplastic exposure had a large and significantly negative effect on all phyla, with chordates (ascidians) most significantly affected ($g = -1.79 [-3.47, -0.12]$, $p = 0.04$), although this result originated from only one study (Anderson and Shenkar, 2021). Echinoderms, crustaceans and molluscs were less, but still significantly, impacted by microplastic exposure, while impacts on annelids and cnidarians were not significant (Fig. 3). Species-level effects were also statistically significant ($Q_{\text{moderators}, 61} = 160.81$, $p < 0.001$). The greatest negative plastics effect on a single species was in the sea urchin *Lytechinus variegatus* ($g = -11.57 [-16.21, -6.92]$, $p < 0.001$, $k = 2$), followed by the coral *Acropora formosa* ($g = -4.67 [-7.22, -2.11]$, $p < 0.001$, $k = 5$).

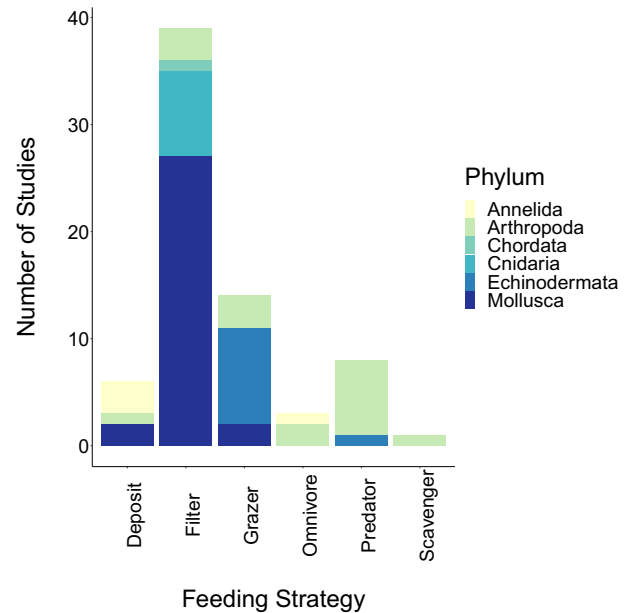


Fig. 1. The frequency of animal feeding strategy by phylum used in 72 experimental studies.

Feeding strategy of the organism contributed significantly to heterogeneity between studies ($Q_{\text{moderators}, 6} = 42.15$, $p < 0.001$) (Fig. 4). Omnivores and deposit feeders experienced the largest negative effects from MPP ($g = -0.93 [-1.69, -0.16]$ and $-0.92 [-1.53, -0.31]$, respectively), while all other feeding strategies except scavengers were also negatively impacted (Fig. 4). Every life stage of organism was significantly negatively impacted by MPP, with earlier life stages most strongly affected, particularly embryos ($g = -1.47 [-2.21, -0.74]$, $p < 0.001$) (Fig. 5).

3.3.2. Microplastic exposure

Microplastic exposure concentration ranged from 1.21×10^{-11} to 1000 g L^{-1} (median = $4.84 \times 10^{-4} \text{ g L}^{-1}$) but did not contribute

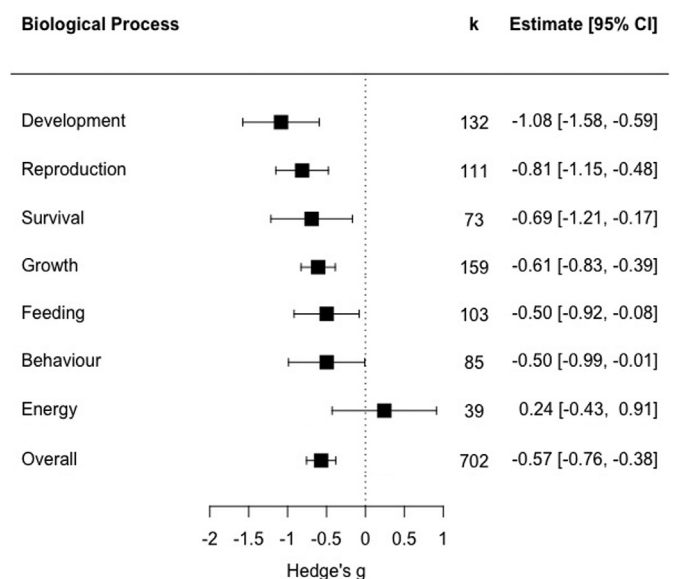


Fig. 2. The effects of microplastic exposure on biological processes of marine benthic fauna. Effects on each of 7 processes and overall, as indicated from random-effects modelling. Boxes and error bars represent pooled Hedge's g values and 95 % confidence intervals, respectively. K represents the number of case studies, or independent experiments within the same study. Overlap of confidence intervals with 0 indicates non-significance.

Table 1

Heterogeneity of effect sizes of microplastics on marine benthic fauna, given as: Wald's Value (I^2), Cochran's value (Q), and the degrees of freedom (DF) and p-value pertaining to Cochran's Q.

Process	I^2 (%)	Q	DF	p-Value
All	61.4	2668.9	700	<0.001
Survival	75.2	658.3	72	<0.001
Feeding	74.4	368.5	102	<0.001
Development	59.4	278.4	131	<0.001
Reproduction	34.2	179.7	109	<0.001
Growth	47.0	602.2	158	<0.001
Energy	80.3	149.4	38	<0.001
Behaviour	73.9	304.2	84	<0.001

significantly to between-study heterogeneity ($R^2 = 0.99$, $Q_{\text{moderators}, 1} = 0.0077$, $p = 0.93$, Fig. S4). However, analysis of the distribution of data showed higher variability in effect sizes at higher concentrations, particularly for fragments (Fig. 6).

The duration for which organisms were exposed to microplastics ranged from 0.17 to 5760 h, with a median duration of 120 h. Meta-regression showed that duration of exposure to microplastics did not explain a significant amount of heterogeneity ($R^2 = 0.02$, $Q_{\text{moderator}, 1} = 0.13$, $p = 0.72$) (Fig. S5a) and the size of microplastic particle did not contribute to variation in effect size ($R^2 = 0.10$, $Q_{\text{moderator}, 1} = 0.08$, $p = 0.77$) (Fig. S5b), although the effects of nanoparticles (<0.1 μm) were not explored in this study.

Microplastic shape accounted for significant heterogeneity in the data (mixed-effect modelling: $Q_{\text{moderators}, 10} = 47.10$, $p < 0.001$), although there was significant residual heterogeneity ($Q_{\text{residual}, 691} = 2543.67$, $p < 0.001$) (Fig. 7). Microplastic fibres, fragments, leachates and spheres had significant negative effects (Fig. 7). Effects driven by microplastic fluff, leachates adsorbed onto microplastics, pellets, powders and squares were not significant, although there were only 3 effect sizes of leachates adsorbed to particles, all from one study (Gu et al., 2020). The most negative significant effect resulted from leachates (no longer adsorbed onto microplastics) ($g = -0.93 [-1.35, -0.51]$, $p < 0.001$), followed by fragments ($g = -0.70 [-1.14, -0.26]$, $p < 0.001$).

From all exposure conditions analysed (MPP concentration, size, shape, exposure duration and polymer type), polymer type contributed the most to between-study heterogeneity ($Q_{\text{moderators}, 19} = 68.93$, $p < 0.001$) (Fig. S6). Polybrominated biphenyl ether had the most negative significant effect ($g = -4.69 [-6.88, -2.51]$, $p < 0.001$) (Fig. S6).

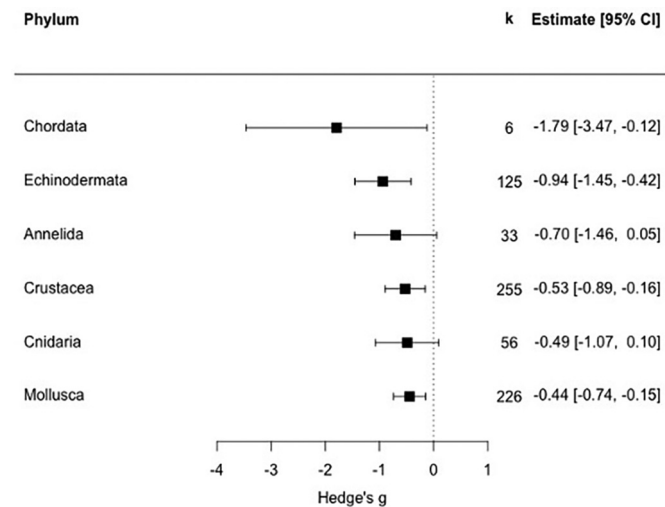


Fig. 3. The effects of microplastic exposure on phyla of marine benthic fauna. Effects on each of 6 phyla as indicated from mixed effects modelling. Boxes and error bars represent pooled Hedge's g values and 95 % confidence intervals, respectively. K represents the number of case studies.

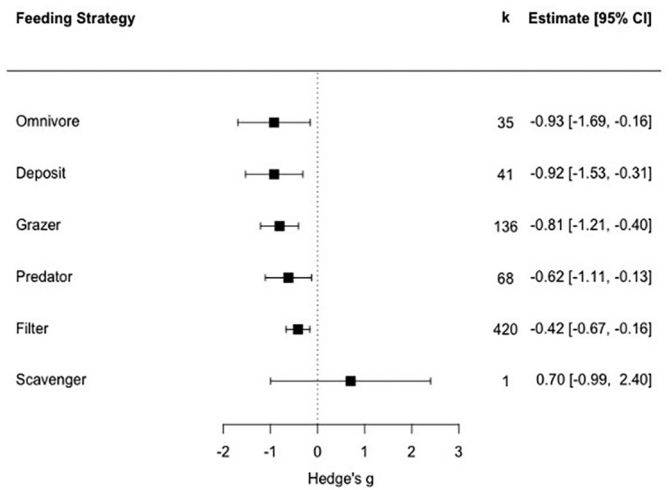


Fig. 4. The effects of microplastic exposure on feeding strategies of marine benthic fauna. Effects on each of 6 feeding strategies, as indicated from mixed-effects modelling. Boxes and error bars represent pooled Hedge's g values and 95 % confidence intervals, respectively. K represents the number of case studies.

4. Discussion

4.1. Biological processes

This study offers the strongest and most consistent evidence to date of an overwhelmingly negative impact of microplastics on marine invertebrates. We found highly significant negative effects of microplastics on the biological process rates of marine benthic fauna. Every life stage was negatively impacted, with the strongest effects on early life stages, especially embryos. There were negative impacts on six out of seven fundamental biological processes including survival, development, reproduction, growth and feeding. Among feeding habits, omnivores and deposit feeders were particularly hard hit. Our study differs from previous reviews in that it documents substantially stronger and more consistently negative impacts of microplastics on a much greater variety of animal life-processes. For instance, Foley et al. (2018) described more neutral than negative effects of microplastics on growth, consumption, reproduction on the survival of fishes and aquatic invertebrates. Previous studies differed in focal organisms from the present study by including freshwater species or fishes (Foley et al., 2018; Salerno et al., 2021; Berlino et al., 2021). Yet, the primary cause for greater predominance of negative impact in the present meta-analysis is likely that the

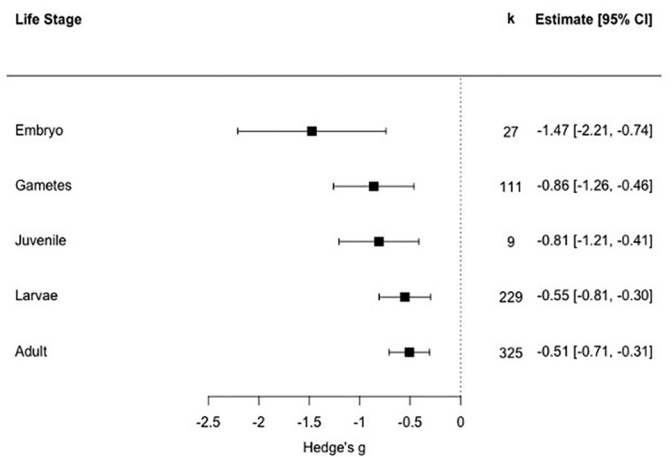


Fig. 5. The effects of microplastic exposure on life stages of marine benthic fauna. Effects on each of 5 life stages as indicated from mixed-effects modelling. Boxes and error bars represent pooled Hedge's g values and 95 % confidence intervals, respectively. K represents the number of case studies.

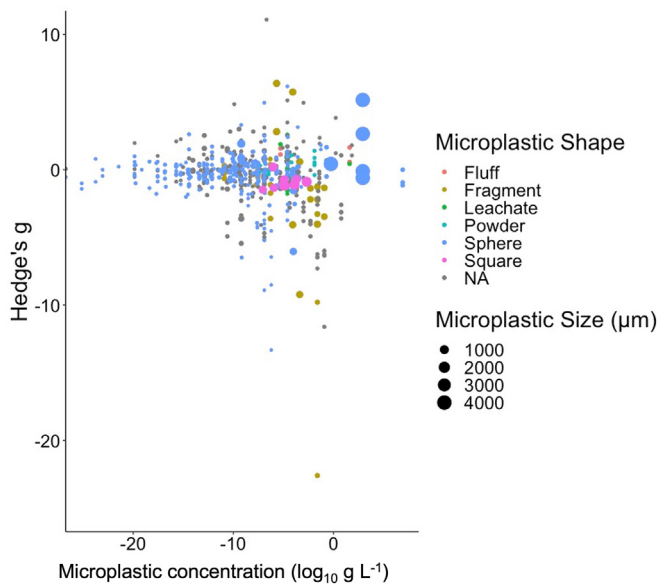


Fig. 6. Effect of microplastic exposure concentration on the biological processes of marine benthos. Effect size indicated by Hedge's g value. Point size is indicative of microplastic particle size, while colour represents the shape of the particle.

rapid increase in experimental studies over the past two years has offered greater statistical power for detecting the impacts of microplastics on marine animals; the present study synthesised data from 72 studies compared to 41 studies in the most recent previous review (Berlino et al., 2021). Certainly, the documentation of negative impacts has become more frequent in recent reviews (Foley et al., 2018; Salerno et al., 2021; Berlino et al., 2021). Our findings of stronger impacts on benthic organisms compared to pelagic and freshwater organisms emphasises the need to improve research efforts in this area.

The reveal that multiple organismal processes and traits are affected by plastics is not surprising. The biological rates of an organism are intrinsically linked and it is unlikely that the effects of microplastics would act independently on each of these. Fig. 8 explores this principle of interlinkages: commencing with the process of feeding, which can be impacted by microplastics as a result of intestinal blockages, false sense of fullness or

confusion with prey (Cole et al., 2011), reduced feeding will limit energy availability for morphological change, gonad development and movement. The suppression of feeding indirectly affects somatic growth, development and reproduction (Foley et al., 2018; Salerno et al., 2021), in addition to direct cellular effects or other growth altering processes such as tissue incorporation (Hierl et al., 2021). The observation that survival was significantly negatively impacted indicates a synergistic effect of plastics on the organism as a whole, wherein the impacts on different processes interact to create a larger combined effect than expected from the sum of individual impacts (Fig. 8). Energy was the only response not significantly impacted by microplastic exposure, which may in part be due to the methodological difficulties in ascribing effects on energetic processes as either positive or negative (Table S5).

4.2. Organism characteristics

Effects of microplastics on benthic taxonomic groups were universally negative, although not significant for annelids and cnidarians. Across multiple taxonomic groups, a reduction in growth was documented, most likely the result of reduced energy reserves as reported by Wright et al., 2013. In that study, a range of exposure concentrations were used, up to 5 % sediment weight. This is likely to be higher than environmentally realistic concentrations of microplastics, perhaps causing more extreme impacts. However, impacts on growth have been seen more widely; previously, 58.8 % of nematodes were shown to suffer energy loss from consuming microplastic particles, particularly fibres (Hodgson, 2018). Growth inhibition may also have resulted from changes in cellular activity (Prinz and Korez, 2020), for instance through cellular modifications (e.g. penetration of microplastics into cell structures) and oxidative stress, although this study focused on organismal level processes rather than cellular. Further research into cellular level effects is therefore strongly recommended.

For several species the strength of impact can be explained by the life stage investigated, although it was not possible to fully disentangle the effects of life stage from species through meta-analysis. The effects of microplastics tends to increase with decrease in organismal size (Salerno et al., 2021), with earlier life stages (gametes, embryos, larvae and juveniles) more severely affected than adults, as recorded here. Thus, the strongest negative effects we recorded were for the larvae of the sea urchin *Lytechinus variegatus*, where abnormal development increased 58.1–66.5 % after microplastic exposure (Nobre et al., 2015). Smaller invertebrates are often numerous and crucial to bottom-up processes in natural ecosystems. Their study is therefore particularly important to predicting the influences of plastic pollution on whole-ecosystem functioning.

The severity of impact from plastics varied with feeding strategy. Omnivores and deposit feeders were most greatly affected, with filter feeders experiencing weaker, but nonetheless significant, negative impacts. Microplastic ingestion varies by feeding strategy (Bour et al., 2018; Naji et al., 2018), with 16 % more microplastics ingested by predators and deposit feeders compared to filter feeders (Bour et al., 2018). The greater ingestion of MPP by predators in particular helps explain the larger negative impacts seen on this trophic group. Our findings were in keeping with Berlino et al. (2021), which also found that benthic filter feeders were negatively impacted by microplastics although, in the earlier study, omnivores, predators and grazers were not. The strong effects on grazers in the present meta-analysis likely resulted from high microplastic concentration on the sediment surface or, in experimental conditions, on the tank floor. Microplastics naturally congregate on the seafloor, with the majority of benthic microplastics found in the top 0.5 cm sediment (Martin et al., 2017), where grazers (and some omnivores) predominantly feed (Duchêne and Rosenberg, 2001). Strong effects of microplastics on predators and omnivores could result from the trophic transfer of microplastics through the food chain, with microplastic fragments being most prone to bioaccumulation (Gray and Weinstein, 2017). The majority of our 72 studies, however, were short-term laboratory experiments, in which study organisms were purchased from aquaria and exposed directly to microplastics, suggesting that trophic transfer would not have influenced

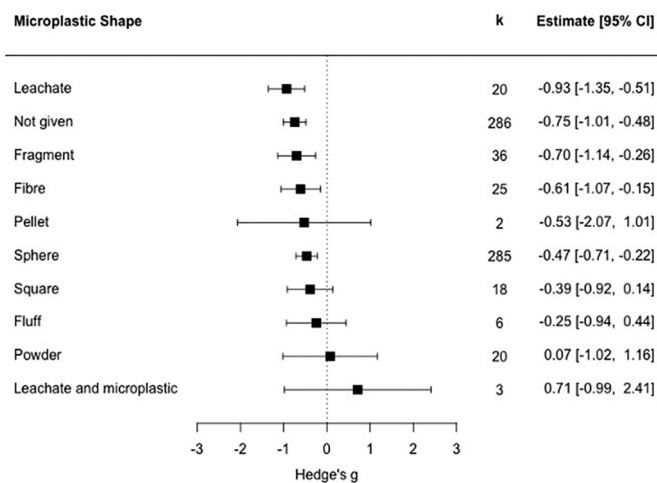


Fig. 7. Responses of benthic fauna to the shape of microplastics used by experiments. Responses indicated from mixed effects modelling. Boxes and error bars represent pooled Hedge's g values and 95 % confidence intervals, respectively. K represents the number of case studies. 'Leachate and microplastic' refers to microplastic particles with adsorbed leachates, while 'leachate' refers to leachate which is not adsorbed to a particle.

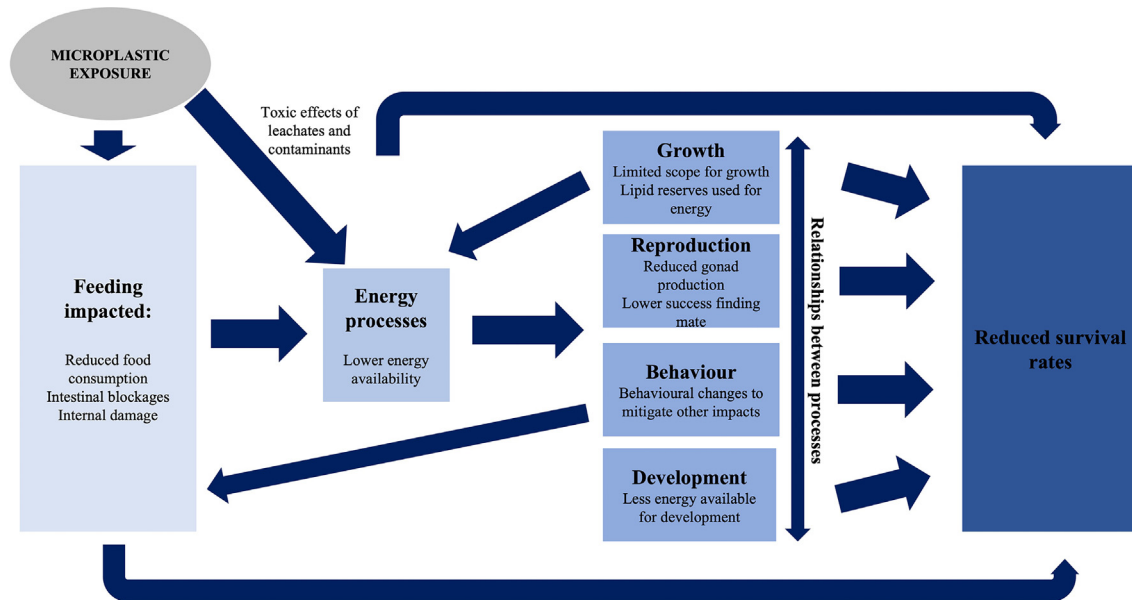


Fig. 8. Interactions of impacts on different biological processes of marine benthic fauna, as a result of microplastic exposure. Interactions demonstrated by arrows, culminating in a synergistic effect and overall reduction in survival rate.

our results and demonstrating a need for more environmentally realistic laboratory experiments.

4.3. Microplastic characteristics

While organismal characteristics were the primary causes for variation in microplastic impact, microplastic shape and polymer type significantly contributed to variation in effect size. We found no effect of microplastic size, exposure concentration and exposure duration, despite individual studies documenting stronger negative impacts at higher exposures (Green et al., 2016; Lo and Chan, 2018). The recorded influence of polymer type conflicted with findings of Lei et al. (2018), where the size of microplastic particle determined toxicity in nematodes and zebrafish and the polymer composition was less important. However, polymer type of a microplastic influences the specific density and hydrophobicity of a particle and thus the biofouling and sinking rates (Kaiser et al., 2017). It is therefore logical that polymer type will influence the availability of both the microplastic itself and its leachates to an organism. In terms of shape, fragments and fibres had larger effects than spheres and squares, potentially, in the case of fragments, due to sharp edges that cause damage following ingestion (Pirsaheb et al., 2020). Fragments and fibres are likely to become the most prevalent microplastics in marine ecosystems, already constituting 48.5 % and 31 %, respectively, of microplastics in sediment and water (Kooi and Koelmans, 2019). The high prevalence of fragments and fibres in marine ecosystems makes the effects of these shapes, compared with spheres, for example, far more environmentally realistic, suggesting that the strong negative impacts of these particle shapes could have widespread implications for benthic ecosystems.

Microplastic dosage had less influence over impacts than microplastic shape or polymer type. This may in part be due to the focus of meta-analytical techniques on average responses, since the influence of microplastic concentration may be more pronounced at extreme values. However, since extreme values are likely to be less environmentally realistic, we consider the use of average values was not detrimental to our conclusions. Of the polymer types investigated, microplastic leachates which had been separated from their microplastic substrates had the strongest negative impacts on fauna. The impacts of leachates on benthic fauna have not been previously investigated by meta-analyses. Leachates included contaminants such as persistent organic pollutants (POPs) which had adsorbed onto the microplastic surface and later been separated, as well as chemicals which has leached directly from the microplastic. Leachates had negative

impacts on reproduction, development and feeding of echinoderms. Leachate endocrine disruptor chemicals (EDCs) can alter hormone production, causing issues such as reduced reproductive success (Gallo et al., 2018). Microplastics with adsorbed benzo[a]pyrene and perfluorooctane sulfonic acid cause more damage to gill tissues and digestive glands compared to non-contaminated microplastics (O'Donovan et al., 2018). On a cellular level, changes to enzyme activity in gobies have been seen following exposure to the antibiotic cefalexin (Fonte et al., 2016), while microplastic associated polychlorinated biphenyls (PCBs) have been shown to contribute to effects such as hepatic stress, tissue accumulation of chemicals, reduced feeding activity and increased mortality (Besseling et al., 2013; Rochman et al., 2013; Herzke et al., 2016). Adsorbed chemicals may therefore have contributed to the negative impacts on feeding activity found by the present study.

4.4. Distribution of literature used

There was a skew in the number of studies by geographic location and sampling taxa. Most studies were published in Europe (49 %) or Asia (24 %), with Africa, North America and South America somewhat under-represented, resulting in a lack of knowledge surrounding native and commercially important species in these regions. The majority of studies analysed were conducted on molluscs that had relevance to human food supply, usually commercially important bivalve species such as the blue mussel, *Mytilus edulis*. For a comprehensive overview to be representative of global impacts, funding should be directed towards addressing the knowledge gaps surrounding continents such as Africa and less commercially important organisms such as polychaetes, for which there is a lack of data. The numbers of relevant studies are increasing rapidly, indicating an opportunity for these knowledge gaps to be filled. Crucially, for findings to be truly comparable there is a need for standardisation of sampling methodology and units of expression, a point widely made in past papers (Hermesen et al., 2018; Miller et al., 2017; Ajith et al., 2020).

5. Conclusions

- Microplastic exposure has significant negative impact on multiple biological processes of marine benthic fauna assessed.
- This study provides the first meta-analytical evidence that microplastic leachates have more severe impacts on benthic fauna than microplastic particles themselves. Clearly, microplastic management should consider

the fate of microplastic already within the marine system, alongside minimising further input.

- Significant knowledge gaps remain surrounding certain geographic regions and species without commercial interest. Future research should be directed towards addressing these gaps.
- A rapid increase in microplastic studies since 2019 caused this study to reveal stronger and more consistently negative effects of microplastics than previous meta-analyses. There is an undeniable and urgent call to address the microplastic crisis within waste management systems globally.

CRedit authorship contribution statement

Victoria G Mason: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Software; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing.

Martin W Skov: Conceptualization; Formal analysis; Funding acquisition; Investigation; Project administration; Resources; Software; Supervision; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing.

Jan Geert Hiddink: Conceptualization; Formal analysis; Funding acquisition; Investigation; Project administration; Resources; Software; Supervision; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing.

Mark Walton: Conceptualization; Formal analysis; Funding acquisition; Investigation; Project administration; Resources; Supervision; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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