Environmental Science & Technology Letters

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Letter

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Evaluating the Drivers of Plastic Ingestion: An Update of the Current Knowledge and an Experimental Approach

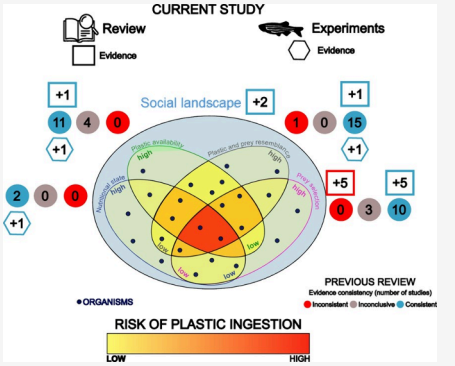
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Cite This: *Environ. Sci. Technol. Lett.* 2026, 13, 281−286

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ABSTRACT: Plastic pollution is rising, widespread, and a threat to biodiversity. Understanding the drivers of plastic ingestion is the key to developing a risk assessment. Although plastic availability, plastic−prey resemblance, degree of food selectivity, and the nutritional state of organisms have been identified as the four main drivers of plastic ingestion, we are still building an evidence base to support these drivers. To strengthen our knowledge of the drivers of plastic ingestion, we used two approaches: a systematic literature review and controlled experiments. Both approaches corroborated these factors as drivers of plastic ingestion, but despite these advances, studies are still needed that address holistic questions applicable to broader scenarios rather than focusing solely on taxon-specific traits or plastic characteristics in isolation from their ecological context. Additionally, a new driver has emerged—the social environment—which adds further complexity to how group formation may affect plastic ingestion across species.



KEYWORDS: *plastic ingestion, pollution, zebrafish, marine debris, behavior ecology, foraging ecology*

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1. INTRODUCTION

Plastic pollution is considered a nearly irreversible threat to the environment and continues to escalate.[1] One of the main reported threats of plastic pollution is its impact on biodiversity. Today over 1500 species are reported ingesting plastics and this number keeps rising.[2] Plastic ingestion is widespread in the tree of life and through the food webs,[2] reported from insects[3] to whales[4] and from zooplankton[5] to rhinos.[6] The impacts of plastic ingestion have been reported from empirical data collected from wildlife as well as from experiments under controlled conditions, spanning from direct death to chronic effects under multiple levels of biological organization.[7]

We are experiencing exponential growth in studies on plastic pollution, but we are still unveiling the relationship between the threats posed by the accumulation of plastics in the environment and the unfolding biodiversity crisis. For instance, the impacts of plastic ingestion at the populational level have been modeled,[8] but they are still far from being understood, mainly due to the chronic nature of the impacts of plastic ingestion. Furthermore, a comprehensive risk assessment of plastic ingestion is still needed. Currently, the risks regarding plastic ingestion are mainly focused on the overlap of plastic pollution and species home range.[9−11] The exposure risk based on the abundance of plastics in the environment may work relatively well for filter-feeding marine megafauna, but the presence of plastic in the environment is one component of the plastic exposure risk, as the presence of plastic pollution in general does not means that the plastic in the environment is in fact available to ingestion.[12] A unified theoretical framework—combining evolution, ecology and behavior under the evolutionary trap concept—proposed that for the evaluation of the risk of plastic ingestion four main drivers may play a role: (i) plastic availability, which is a combination of the volume and distribution of plastics in the environment with the foraging strategies of organisms; (ii) the level of prey resemblance with plastic; (iii) the degree of food selectivity of a species, spanning from generalist to specialist; (iv) nutritional state of the individual, which is related to the risk of starvation and the level of hunger.[2] However, the number of studies providing empirical evidence regarding these drivers is limited, even with regard to the relationship between plastic abundance and plastic ingestion. By 2021, when the theoretical framework was proposed, 10 to 15 studies supported each of the drivers, except for the nutritional state, which was supported by only two studies. This knowledge gap is critical,

Received: December 15, 2025
Revised: January 8, 2026
Accepted: January 9, 2026
Published: January 20, 2026



ACS Publications

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as understanding the drivers of plastic ingestion is key to developing a more precise understanding of the threats posed to biodiversity. To that end, we evaluate the drivers of plastic ingestion using two approaches: (i) a review of current knowledge on the evidence of each of the proposed four main drivers and (ii) an experimental study using zebrafish (*Danio rerio*), a prominent vertebrate model,[13] designed to evaluate the relationship between plastic ingestion and plastic availability, plastic and prey resemblance, and the nutritional state of animals. The degree of food selectivity, a driver that requires interspecific comparisons, was not experimentally tested and was therefore addressed exclusively through the literature.

2. MATERIALS AND METHODS

2.1. Review of Current Knowledge on the Drivers of Plastic Ingestion

The first review dedicated to identifying the main drivers of plastic ingestion included 1,228 papers published between 1981 and 2020. To update current knowledge on the main drivers of plastic ingestion, we surveyed literature published between 2021 and May 2025, indexed in the Web of Science Core Collection (all editions), searching in all searchable fields using the following keywords: "microplastic* INGESTION" OR "nanoplastic* INGESTION' OR "macroplastic* INGESTION" OR "mesoplastic* INGESTION" OR "PLASTIC* INGESTION". We systematically reviewed only peer-reviewed research articles, excluding reviews, proceeding papers, meeting abstracts, and other types of documents. We quantified the number of studies and classified them based on: (i) the type of study (field or experiment); (ii) the taxonomical group (e.g., invertebrates, fishes, reptiles, or birds); (iii) the type of ecosystem (terrestrial, freshwater, or marine); (iv) evidence consistency (consistent, inconclusive, or inconsistent). To be considered in our analysis, the study must have performed a statistical analysis to evaluate one of our drivers of plastic ingestion: plastic availability, the level of prey resemblance with plastic, the degree of food selectivity of a species, and nutritional state of the individual.

2.2. Zebrafish Experimental Design

2.2.1. Zebrafish Maintenance. Wild type adult zebrafish were purchased from a local aquarium supplier. The maintenance of animals followed standard protocols[14] and all experimental procedures were approved by the Ethics Committee on Animal Experiments – UFAL (#10/2022). Prior to experiments, all fish underwent an acclimation period for 10 days and were fed exclusively with saline *Artemia* nauplii. A total of 720 adults of zebrafish were used in the three different experiments described in the following sections. Each experimental unit consisted of one 4.8 L aquarium containing 15 animals, and each treatment included 5 replicates. A balance of 8 females and 7 males was maintained in each experimental aquarium, resulting in a mixed experiment with an approximately 1:1 sex ratio. After each experiment all animals were euthanized, and the intestine was dissected to quantify the ingested microplastics. Detailed information about zebrafish maintenance, feeding, acclimation period, and euthanasia are described in the Supporting Information.

2.2.2. How Does Plastic Availability Influence Plastic Ingestion? To evaluate the effect of plastic availability on plastic ingestion in zebrafish, they were exposed to three different microplastic concentrations: low (0.0001 g/L, equivalent to 8 particles/L), medium (0.001 g/L, equivalent to 80 particles/L), and high (0.01 g/L, equivalent to 800 particles/L). All animals were maintained under the same feeding regime. The microplastic used in this experiment was red polyethylene (PE) microspheres (UVPMS-BR-1.090), with sizes ranging from 250 to 300 μm, purchased from Cospheric Inc. (North Carolina, USA). Detailed information on the pre-experimental protocol, feeding regime, control aquariums, and quantification of microplastics is described in the Supporting Information.

2.2.3. How Does Plastic and Prey Resemblance Influence Plastic Ingestion? To address the question of how plastic resemblance to prey affects plastic ingestion, and considering that zebrafish primarily use vision to guide foraging behavior,[15] we exposed fish to two different plastic colors: red, the same microsphere used in the previous experiment, and blue (UVPMS-BB-1.13), a PE microsphere of the same size as the red microplastic. We considered the red microsphere to more closely resemble *Artemia* (the food item used to feed the animals throughout the experiment) and zooplankton species (a major food item in the wild zebrafish diet[16]) than the blue particle. In this experiment, we had three treatments in which animals were exposed for 1 h to (i) red microplastic only, (ii) blue microplastic only, and (iii) red and blue microplastic in the same proportion. In all treatments, animals were exposed to a concentration of 0.001 g/L of microplastic, which was offered together with the *Artemia* nauplii. Detailed information on the pre-experimental protocol, feeding regime, control aquariums, and quantification of microplastics is provided in the Supporting Information.

2.2.4. How Does Nutritional State of Individuals Influence Plastic Ingestion? To evaluate the effects of nutritional state on plastic ingestion, animals were exposed to microplastic (0.001 g/L) during 1 h following four different fasting regimes: 30 min, 1 h, 2 h, and 24 h. The effects of the fasting treatments on plastic ingestion were evaluated independently for red and blue microspheres. Detailed information on the pre-experimental protocol, feeding regime, control aquariums and microplastic quantification are described in the Supporting Information.

2.2.5. Statistical Analysis. We used mixed generalized linear models (GLMMs) with a Poisson distribution suitable for count data to evaluate different aspects of plastic ingestion in zebrafish. Response variables included the total amount of plastic, the amount of plastic by color, and the number of plastic particles per individual, depending on the analysis. Predictor variables varied by analysis: plastic availability (three levels), particle color, fasting time (T1–T4), and relevant interactions. Fish identity nested within the aquarium receiving the treatment was included as a random effect. Models were fitted by using the glmmTMB() function from the glmmTMB package. Differences between treatments were evaluated using the emmeans() function, specifying type = "response" to obtain estimates on the original response variable (count). Subsequently, pairwise comparisons between factor levels were performed by using the pairs() function, applying the Bonferroni correction for multiple comparisons. All analyses were performed in R (R Core Team, 2023).

3. RESULTS AND DISCUSSION

We systematically reviewed 1,134 papers, and studies directly addressing the drivers of plastic ingestion are still rare (9 papers) compared to the ever-growing number of papers reporting and describing ingestion or the potential effects of plastic ingestion. We now have 53 papers (43 from the previous review, nine from the current review, and the experimental approach of the present study) directly addressing the drivers of plastic ingestion. Although there are a large number of papers addressing plastic ingestion, we identified a consistent conceptual gap: many studies attempt to relate the amount of plastic present in the environment to ingestion, but this is not equivalent to testing the influence of plastic availability. Not all plastic in the environment will in fact be available to ingestion,[2] and therefore environmental abundance alone cannot be used as a proxy for availability. Additionally, plastic availability is one factor that influences the risk of plastic ingestion, and controlling the other variables in the natural environment is a great challenge, which will demand sampling multiple populations under different plastic abundances.[12] Regarding this drive, we found one experimental study that was consistent with the theoretical framework, where the highest plastic ingestion by sea cucumbers was

https://doi.org/10.1021/acs.estlett.5c01241
Environ. Sci. Technol. Lett. 2026, 13, 281–286

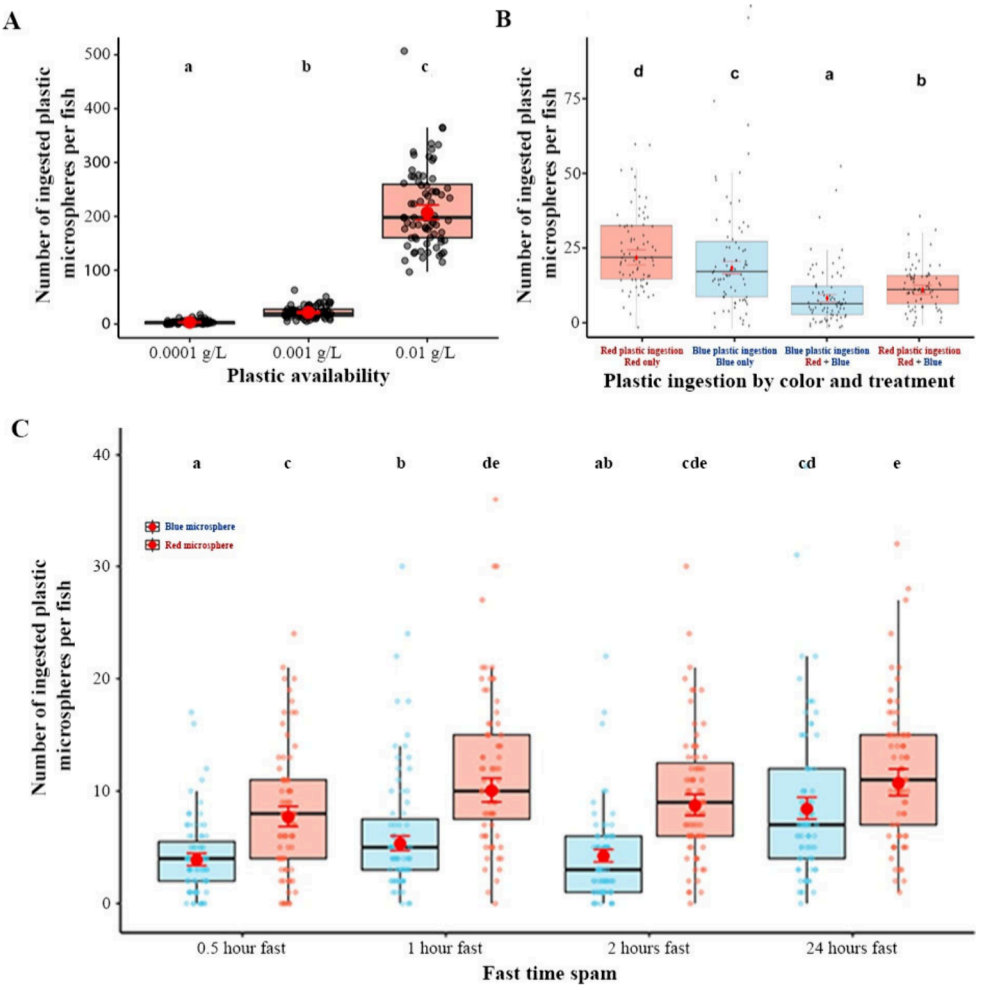


Figure 1. Microplastic ingestion by *Danio rerio* (zebrafish)under different experimental conditions. (A) Number of microspheres ingested per fish at three levels of plastic availability (0.0001, 0.001, 0.01 g/L)—experiment A. (B) Ingestion of red and blue microspheres across different treatments—experiment B. (C) Number of microspheres ingested per fish after different fasting times (0.5, 1, 2, 24 h)—experiment C. Red circles represent the mean ± standard error. Blue boxplots correspond to the ingestion of blue microspheres and red boxplots to the ingestion of red microspheres. For all figures different letters above the boxplots indicate significant differences among treatments, $\alpha = 0.05$). The lowest means are always represented by the letter "a" and increase following the alphabetical sequence.

recorded under the high microplastic concentration.[17] Our results from the experiment designed to test the influence of plastic availability on plastic ingestion were also in line with the proposed framework, with significant differences among the treatments (χ^2= 25,69, d.f. = 2, $p < 0.0001$; Figure 1A; Tables S1 and S2). At the lowest level of plastic availability, the mean number of PE microspheres ingested per fish was 3.36. At the intermediate level, corresponding to a 10-fold increase in availability, the mean number of particles ingested was 21.46, a 6.3-fold increase. At the highest level of availability, representing a 100-fold increase relative to the lowest level, the mean ingestion reached 207.1 particles per individual, approximately 60 times higher than ingestion at the lowest availability level. The increase in plastic ingestion was not linear in relation to the increase of plastic availability; this is expected as there are foraging and handling costs for additional items[18] and plastics have no nutritional value.

Plastic—prey resemblance is one of the oldest and most widely discussed drivers of plastic ingestion,[19] both by the general public and the scientific community. A well-known example is the jellyfish hypothesis, which suggests that sea turtles ingest plastic due to the similarity to jellyfish. This driver had the strongest and most consistent support in the previous review;[2] however, we find only one paper using fish directly testing this relationship,[20] which corroborated the theoretical framework. Despite finding only one paper directly testing plastic—prey resemblance as a driver, recent literature continues to demonstrate plastic selectivity by wildlife, particularly with respect to color.[21,22] An interesting finding regarding color preference—although it involved manipulated edible jellyfish rather than actual plastics—was that sea turtles' preferences changed according to the color of their primary food in captive environments.[21] These findings suggest that animals' perception of prey may vary according to local experience. Our experimental results on plastic—prey resemblance also corroborated that the similarity of plastic to natural food positively influenced the ingestion of plastic particles by organisms (χ^2 = 142.13, d.f. = 3, $p < 0.0001$; Figure 1B; Tables S3 and S4). In the treatment where only red particles (more similar to prey) were available, the highest mean ingestion was observed, with 19.95 particles per individual. In the treatment with exclusively blue particles (less similar to prey), the mean ingestion was 17.10 particles, representing a reduction of approximately 14% compared to the red-only treatment. When

https://doi.org/10.1021/acs.estlett.5c01241
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both red and blue particles were offered simultaneously, a clear preference was observed: the mean ingestion of red particles was 10.84, while the ingestion of blue particles was even lower, averaging 8.51 particles per individual. These values represent reductions of approximately 46% and 57%, respectively, compared to those of the red-only treatment.

The nutritional state of an individual may influence plastic ingestion by broadening the range of accepted food items, which can reduce foraging performance and lead to the consumption of less-profitable foods.[2] Some process may trigger this broad acceptance, such as level of hunger and the risk of starvation.[23] The nutritional state as a driver of plastic ingestion is the least studied factor, and in our review, we did not find any additional studies on the relationship between starvation risk and plastic ingestion. However, one study reported that starvation is linked to the ingestion of nonfood items (pumice) by short-tailed shearwaters.[24] Although the authors could not test the relationship between starvation in short-tailed shearwaters and plastic ingestion, the same mechanism that induced pumice ingestion may also apply to plastic ingestion. Our experiments on the role of hunger as a driver of plastic ingestion showed that fasting time significantly influenced the ingestion of plastic particles by the organisms (χ^2= 447.75, d.f. = 7, $p < 0.0001$; Figure 1C; Tables S5 and S6). When comparing the number of particles ingested between the shortest (0.5 h) and longest (24 h) fasting periods, we found a significant difference, with higher ingestion values after the longest fasting period. We found a similar pattern of ingestion across fasting periods for both blue and red particles, with higher ingestion of red particles compared to that of blue particles in all fasting treatments. Additionally, we found an interaction between plastic resemblance to food and fasting time, in which plastic particles that were more similar to the food (red particles in our experiment) needed the shortest fast time to be highly ingested in comparison to plastic particles that held less resemblance with food (blue particles in our experiment).

Feeding ecology is another common trait explored as a driver of plastic ingestion in the recent literature, but animals are rarely clearly classified along the generalist−specialist spectrum. Animals, especially fishes, are often classified according to their ecological guilds,[25−30] which is informative but difficult to extrapolate into a broader framework applicable to both terrestrial and aquatic animals regardless of taxonomy. We found six studies that test more directly the relationship between generalist feeding behavior and plastic ingestion (Table S7). One study found that marine herbivorous fishes ingested more plastic than omnivorous fish, which is inconsistent with the idea that animals with broader diets are more prone to ingest plastic due to their lower acceptance threshold.[31] The authors suggested that this difference may be due to feeding habitat: herbivorous fish were grazing in areas where microplastics tend to accumulate, thus being exposed to higher levels of plastic availability. Another possible explanation proposed by the authors was that the morphology of the gastrointestinal tract of herbivorous fish favors the retention of microplastics, thereby contributing to their higher plastic ingestion counts. The other five studies were consistent with the proposed framework, showing that more generalist animals ingested more plastic: two involved marine fishes,[32,33] one estuarine fishes,[34] one seabirds,[35] and one marine zooplankton species.[36] The taxonomic diversity covered by these studies supporting this driver highlights its robustness and reinforces the need to examine plastic ingestion under ecological lenses. One innovation identified in the literature review was the use of the isotopic trophic niche as a tool to explore the relationship between feeding ecology and plastic ingestion, with wider isotopic niches being associated with higher plastic ingestion.[32,35] The use of the isotopic niche is a useful approach, as it provides quantitative values along the specialist−generalist spectrum, rather than only categorical ones (e.g., omnivorous or herbivorous), and is relatively easier to implement compared to detailed diet analysis.

One additional driver of plastic ingestion identified in our review was the social environment.[37,38] Interpreting plastic ingestion within the theoretical framework of the evolutionary trap raises the question of how social interactions may influence this process, as group living can increase competition for resources.[39] Group size and dynamics may influence the selection of novel or nonoptimal items, with dominant and subordinate individuals potentially behaving differently when exposed to them.[37] Two studies investigated the influence of social interactions on plastic ingestion using fish as the animal model (Table S7), and both found that group dynamics affected plastic ingestion.[37,38]

Although our understanding of the drivers of plastic ingestion has advanced in recent years, more information is still needed to build a robust risk assessment. Studies should be designed so that their results can be extrapolated beyond the model species, addressing broader questions rather than focusing solely on taxon-specific traits (e.g., trophic guilds) or plastic characteristics (e.g., color) in isolation from their ecological context. Additionally, care must be taken when testing the influence of environmental plastic on ingestion, as not all plastics present in the environment are actually available for ingestion, due to their characteristics or the foraging behavior of organisms.[12] There is also a need to further explore the relationship between the social environment and plastic ingestion in order to understand whether group formation enhances the likelihood of plastic ingestion. Understanding the factors linked to exposure to and impact of plastic pollution on wildlife is key to developing a risk assessment of the plastic ingestion threat and to designing mitigation actions, in which the drivers of plastic ingestion are central to understanding exposure

■ ASSOCIATED CONTENT

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.estlett.5c01241.

Scripts for statistical analysis and data sets, pre-experimental protocol, feeding, acclimation, and animal maintenance protocols, data from the control experiment, and euthanasia procedures (PDF)

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https://doi.org/10.1021/acs.estlett.5c01241
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Funding

The Article Processing Charge for the publication of this research was funded by the Coordenacao de Aperfeicoamento de Pessoal de Nivel Superior (CAPES), Brazil (ROR identifier: 00x0ma614).

Notes

The authors declare no competing financial interest.

■ ACKNOWLEDGMENTS

This work was funded by FAPEAL-Research Support Foundation of the State of Alagoas (#60030.0000001751/2022) and in part by the Coordination for the Improvement of Higher Education Personnel CAPES-Brazil (CAPES-Finance Code 001) and by the National Council for Scientific and Technological Development (CNPq) (#405449/2022-4, CNPq/MCTI-FNDCT CT-Petro N 43/2022). R.G.S. was funded by CNPq (research productivity grant # 312099/2023-1).

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https://doi.org/10.1021/acs.estlett.5c01241
Environ. Sci. Technol. Lett. 2026, 13, 281−286