Environmental Toxicology

Parasites and Pollutants: Effects of Multiple Stressors on Aquatic Organisms

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Abstract: Parasites can affect their hosts in various ways, and this implies that parasites may act as additional biotic stressors in a multiple-stressor scenario, resembling conditions often found in the field if, for example, pollutants and parasites occur simultaneously. Therefore, parasites represent important modulators of host reactions in ecotoxicological studies when measuring the response of organisms to stressors such as pollutants. In the present study, we introduce the most important groups of parasites occurring in organisms commonly used in ecotoxicological studies ranging from laboratory to field investigations. After briefly explaining their life cycles, we focus on parasite stages affecting selected ecotoxicologically relevant target species belonging to crustaceans, molluscs, and fish. We included ecotoxicological studies that consider the combination of effects of parasites and pollutants on the respective model organism with respect to aquatic host–parasite systems. We show that parasites from different taxonomic groups (e.g., Microsporidia, Monogenea, Trematoda, Cestoda, Acanthocephala, and Nematoda) clearly modulate the response to stressors in their hosts. The combined effects of environmental stressors and parasites can range from additive, antagonistic to synergistic. Our study points to potential drawbacks of ecotoxicological tests if parasite infections of test organisms, especially from the field, remain undetected and unaddressed. If these parasites are not detected and quantified, their physiological effects on the host cannot be separated from the ecotoxicological effects. This may render this type of ecotoxicological test erroneous. In laboratory tests, for example to determine effect or lethal concentrations, the presence of a parasite can also have a direct effect on the concentrations to be determined and thus on the subsequently determined security levels, such as predicted no-effect concentrations. *Environ Toxicol Chem* 2023;42:1946–1959. © 2023 The Authors. *Environmental Toxicology and Chemistry* published by Wiley Periodicals LLC on behalf of SETAC.

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INTRODUCTION

In ecotoxicological studies, various test organisms are used for either laboratory or field investigations to assess the effects of pollutants at various levels. In many cases, these test organisms might be infected by parasites. In fact, it is estimated today that the number of parasite species ranges from one third to over one half of the earth's total biodiversity (Poulin, 2014; Poulin & Morand, 2004), therefore parasites are common in most field-collected test organisms used to study

toxicant effects. Because parasites often act as an additional stressor, they will likely affect the outcome of ecotoxicological studies (Marcogliese & Pietrock, 2011; Sures et al., 2023; Sures, Nachev, Selbach, et al., 2017). Adverse effects of parasites on the health of their hosts can usually be expected given the fact that they have long been recognized as important pathogens of different organisms, among them humans and livestock (Sures, Nachev, Pahl, et al., 2017). The harm associated with parasites has long been the main reason to study parasites, which ended up in a wealth of medical and veterinary textbooks about their pathogenic effects and their possible treatment. Following this initial awareness of parasites several key studies demonstrated the wide distribution of parasites in wild animals and gave examples of their ecological implications and effects on ecosystem processes (e.g., Hudson et al., 2006; Poulin, 1999; Timi & Poulin, 2020; Tompkins et al., 2011; Wood & Johnson, 2015). In this context, it has to be noted that effects

are often more severe for intermediate hosts compared with the final host in the life cycle, particularly if the parasite is trophically transmitted. Furthermore, some parasites do not cause obvious effects on their hosts (Øverli & Johansen, 2019).

According to our common understanding, we can define a parasite as an organism that lives in or on another organism of a different species (host) and has some effect on the host that has mostly a negative, but sometimes also a positive, effect on the host fitness (Bollache et al., 2002; Cornet et al., 2009; Giari et al., 2020; Helluy, 2013; Jacquin et al., 2014; Marcogliese, 2004, 2005; Piscart et al., 2007; Sures, Nachev, Pahl, et al., 2017; Thomas et al., 2000). Although this definition might also include bacteria and viruses, the word "parasites" as opposed to "pathogens" often refers only to eukaryotic organisms. In the following sections, we use the term "parasite" in this sense. Besides the consumption of host resources, parasites can modulate various host body functions such as the immune and hormone system, metabolism and energy storage, the general stress response (e.g., heat shock protein 70 [hsp70], cortisol), oxidative stress, and other biomarkers (Ford & Fernandes, 2005; Marcogliese & Pietrock, 2011; Minguez et al., 2009; Morley, 2006; Poulin, 1992; Sures, 2006, 2008a, 2008b; Sures, Nachev, Selbach, et al., 2017; Tekmedash et al., 2016). In addition, several parasites can accumulate toxicants and can reduce the tissue concentrations in the host, which might, as a consequence, lead to a different stress response in infected versus uninfected hosts (Nachev & Sures, 2016; Sures & Nachev, 2022; Sures et al., 2023). Before going into details with respect to possible parasite–pollutant interactions and their combined effects on hosts and ecotoxicologically relevant parameters, we will give a brief overview of the most important groups of parasites occurring regularly in selected ecotoxicological target species belonging to crustaceans, molluscs, and fish.

ECOTOXICOLOGICALLY RELEVANT PARASITE TAXA

Some parasite groups occur frequently in test organisms that are used in ecotoxicological studies and can have a significant impact on the response to further stressors. We briefly summarize the life cycles of the major parasite groups that are relevant for our review.

Microsporidia

Taxonomically, the Microsporidia are closely related to the fungi and belong to the group Opisthosporidia (Bojko et al., 2022). They can parasitize a wide variety of hosts, including crustacea and other invertebrates or fish, where they develop intracellularly in various tissues, depending on the microsporidian species. Transmission can be horizontally from one host to the next or vertically via the gonads from mother to offspring (Dunn et al., 2001; Smith, 2009; see Figure 1 for details). Because microsporidia cannot usually be detected by the naked eye in their hosts, molecular analyses are necessary to determine the infection status of the studied free-living species (e.g., Link et al., 2022).

Plathelminthes

The parasitic plathelminths comprise the Monogenea (skin flukes), Cestoda (tapeworms), and Trematoda (flukes). Monogeneans are mostly ectoparasites (flatworms of gills or skin) of aquatic organisms like fish or amphibians (Figure 2A–C). They have simple life cycles using a single host species and without asexual reproduction (Figure 2A). Some species are oviparous,
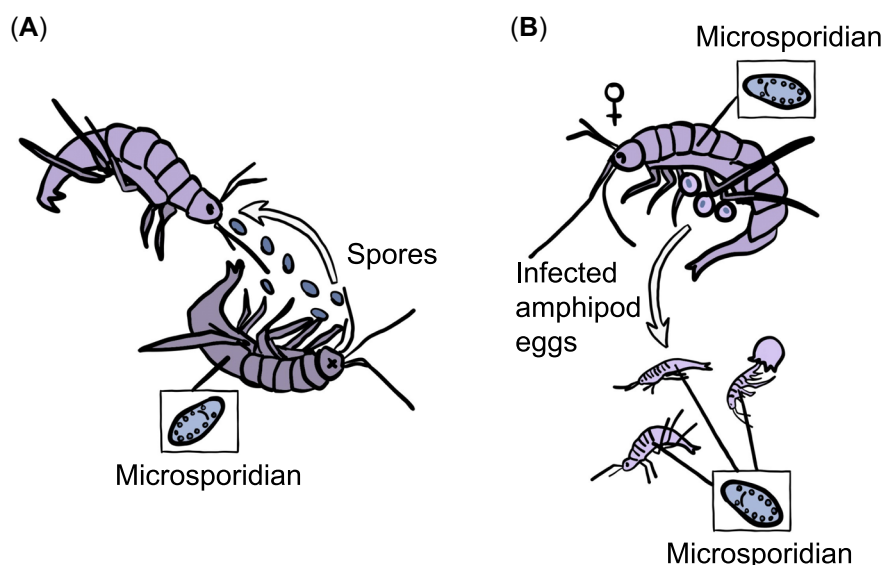

FIGURE 1: Life cycle of microsporidians with (**A**) horizontal and (**B**) vertical transmission. (**A**) Horizontally transmitted microsporidians are usually more pathogenic, and development of spores leads to host death and release of spores to the environment, where they are taken up by uninfected amphipods. (**B**) In the case of vertical transmission, stages of the parasite enter the eggs via the ovary of the female and are transmitted to the offspring. Vertically transmitted microsporidians are dependent on the host reproduction and will not have a significant impact on the survival of their host (Dunn et al., 2001). Nevertheless, these parasites can modulate the sex ratio of their host population by either male killing or feminization (e.g., amphipods; Haine et al., 2007; Smith, 2009; Stentiford & Dunn, 2014).
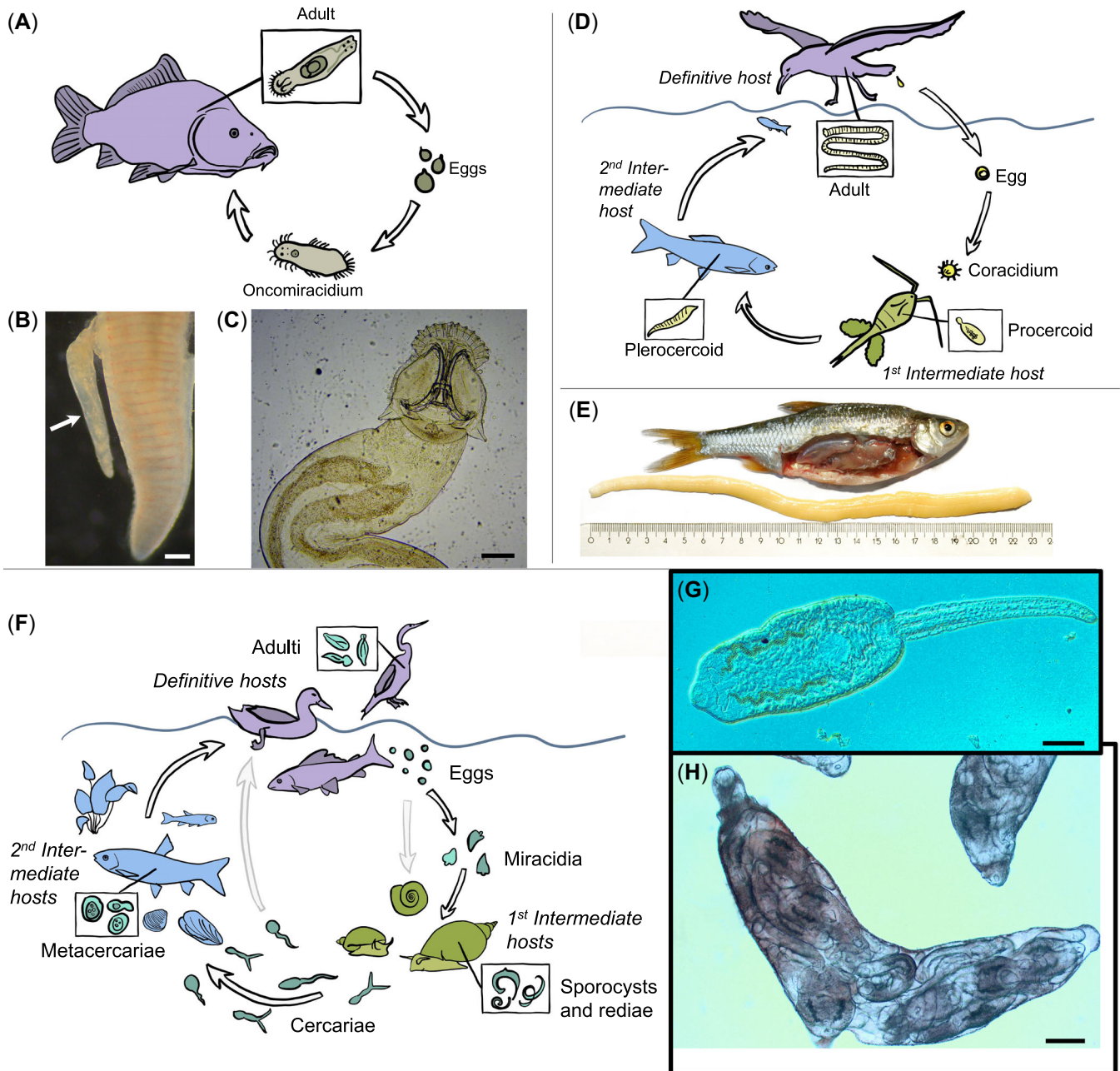
FIGURE 2: Life cycles of parasitic plathelminths. (**A**) Life cycle of monogenean. Adult parasites live on fish and reproduce. Eggs are released to the water and an Oncomiracidium hatches that actively locates a new fish host, attaches, and develops to the adult. (**B**) *Macrodactylogyrus congolensis* attached to the gill filament of *Claris gariepinus* (arrow). Scale bar 500 μm. (**C**) Opisthaptor of *M. congolensis*. Scale bar 200 μm (photographs in 3B and 3C by N. Smit). (**D**) Life cycle of the cestode *Ligula intestinalis*. Adult cestodes in the intestine of a fish-eating bird. Eggs are released with faeces from the bird and coracidium larva hatches in water. The coracidium is consumed by a copepod and develops in its hemocoel to the procercoid larva. A fish (second intermediate host) is consuming the infected copepod and the larva migrates to the body cavity, where it develops to the large plerocercoid larva. Birds get infected by feeding on infected fish containing the plerocercoids. The cestode larva matures in the bird intestine and adult worms reproduce sexually (Gutiérrez & Hoole, 2022). (**E**) Plerocercoid larva of *L. intestinalis* dissected from the body cavity of roach. (**F**) Generalized life cycle of Trematoda. Eggs are released by the definitive host. The next host (first intermediate host) is a mollusc, in most cases a snail, that gets infected by ingesting the parasite eggs or miracidia (the larval stage that hatches from eggs). In the snail, the parasite develops into sporocysts and/or rediae (depending on trematode species) and multiplies asexually. Large numbers of free-swimming larval stages (cercariae) are produced and released to the water where (depending on the trematode species) they infect a second intermediate host, encyst on plants or other organisms (e.g., shells of snails), or are directly infective for the final vertebrate host where the parasite reproduces sexually (Esch et al., 2002). (**G**) Cercaria of *Echinostoma recurvatum*. (**H**) Redia of *E. recurvatum* containing developing cercariae. Scale bars 100 μm. Photographs: J. Schwelm.

producing eggs that release a free-swimming larval stage called oncomiracidium, while some species are viviparous. On the host, the adult monogeneans attach with a posterior structure, the opisthaptor bearing hooks and/or suckers (Figure 2B,C), and feed on mucus, epithelial cells, or blood (Bakke et al., 2007; Buchmann & Bresciani, 2006). Monogenean populations were found to react strongly to environmental stressors like metals or eutrophication (Gilbert & Avenant-Oldewage, 2021) and were

found to respond to environmental pollution (Sanchez-Ramirez et al., 2007).

In contrast to monogeneans, adult cestodes (tapeworms) live in the host intestine. These parasites can have complex life cycles with details that can vary largely depending on the cestode species (Figure 2D,E). For example, the cestode *Ligula intestinalis*, a parasite that interfers with the hormone balance of its fish intermediate host, has a life cycle including a copepod, a fish intermediate host, and a bird as the final host (Figure 2D). *L. intestinalis* has a strong influence on the hormone system of the fish and thereby interferes with host reproduction (Schabuss et al., 2005; Trubiroha et al., 2010).

The life cycles of trematodes involve a vertebrate final host and one or two intermediate hosts, including a phase of massive asexual multiplication in the first intermediate host (mostly snail; see Figure 2F–H for details).

Acanthocephala

The exclusively parasitic helminth group Acanthocephala is also called "thorny-headed worms." These parasites have life cycles that involve an invertebrate intermediate host (e.g., amphipods) and a vertebrate final host (e.g., fish; Kennedy, 2006; Perrot-Minnot et al., 2023; see Figure 3 for details). The cystacanth larvae (Figure 3B) often manipulate the behaviour of their invertebrate intermediate host by interfering with host physiology to enhance the trophic transmission to the final host (Helluy, 2013) and thereby execute a variety of physiological effects (e.g., Bailly et al., 2018; Bakker et al., 2017; Bollache et al., 2000; Cornet, 2011), which might also be important for ecotoxicological studies (Grabner & Sures, 2019). Adult acanthocephalans (Figure 3C) are known to accumulate enormous amounts of metals inside their bodies, often exceeding the concentrations detected in the organs of their fish hosts (Sures & Nachev, 2022). This enormous metal accumulation might even lead to reduced metal concentrations in tissues of infected hosts as compared with uninfected ones (see Sures, Nachev, Selbach, et al., 2017; Sures et al., 2023, and references therein), suggesting that adult acanthocephalans might be beneficial to their hosts under polluted conditions.

Nematoda

Not many nematodes (also called roundworms) have been studied in an ecotoxicological context so far. One species for which additional stressor effects on the host are comparatively well studied is the eel nematode *Anguillicola crassus*. This parasite is an invasive eel parasite in Europe and other parts of the world, and uses different species of copepods as intermediate hosts (see Figure 4 for details). As adults, these nematodes suck blood from the capillaries inside the swim bladder of eels and are therefore considered a serious threat to the population of European eels (Sures & Knopf, 2004).

PARASITES AND POLLUTANTS AS MULTIPLE STRESSORS

When parasitized test organisms are exposed to additional stressors such as pollutants, they are subjected to multiple stressors (Sures et al., 2023). The effects of the combined stressors might be different compared with what can be expected from each single stressor. Conceptually, there can be different scenarios when dealing with two stressors (Figure 5): First, one of the stressors can be dominant and override
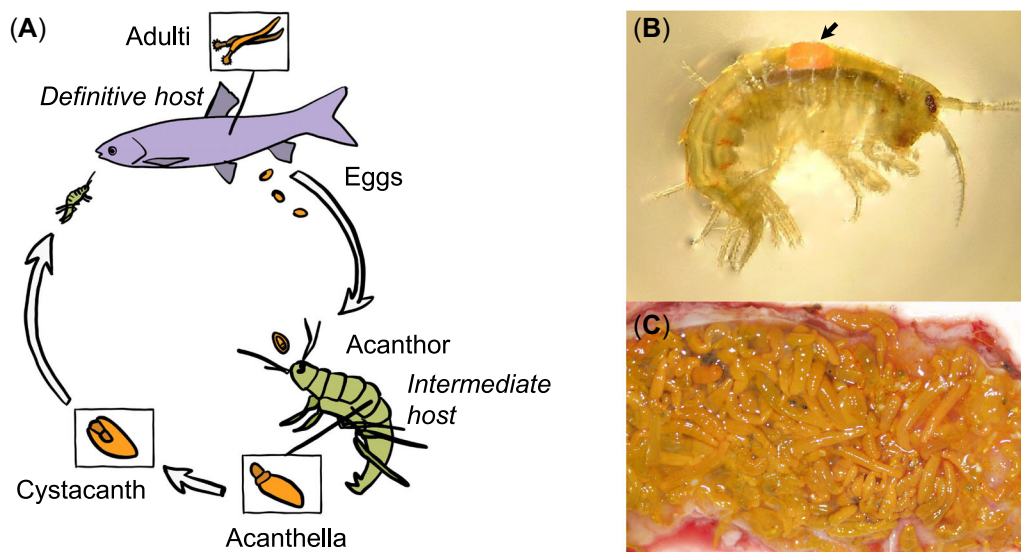

FIGURE 3: (**A**) Life cycle of the acanthocephalan *Pomphorhynchus* sp. In the fish final host, the adult parasite lives in the intestine and reproduces sexually. The females lay eggs that are released with the host faeces and are infective for the intermediate host that takes up the eggs containing the acanthor stage orally (Taraschewski, 2000). In the amphipod intermediate host, the parasite develops to the acanthella and later to the cystacanth stage, which is trophically transmitted to the fish. (**B**) Infected amphipod with cystacanth larva in the body cavity that can grow to a considerable size compared with the host and is visible from the outside in the living host (arrow). (**C**) Opened fish intestine with heavy infection of *Pomphorhynchus* sp.
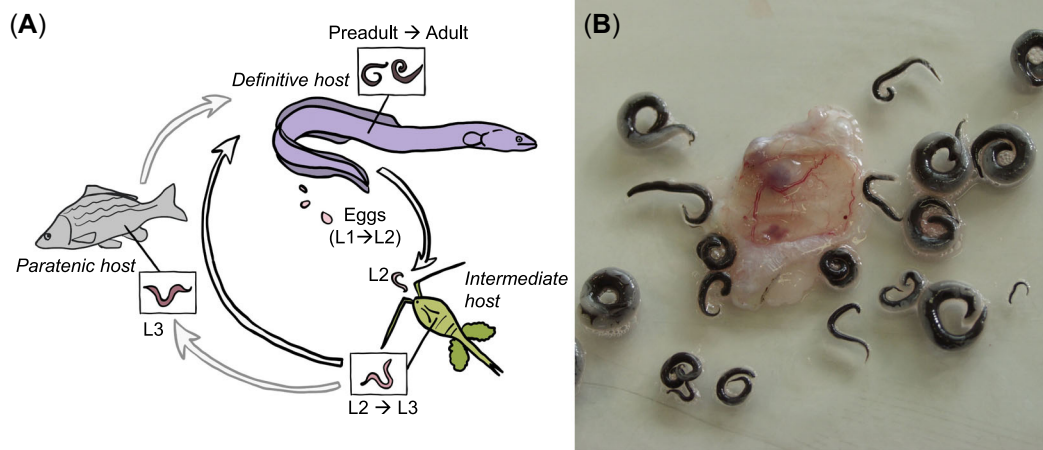
FIGURE 4: Life cycle of the eel nematode *Anguillicola crassus*. (**A**) Life cycle including the eel final host where the adult nematodes live in the swim bladder and reproduce sexually. Eggs are released with eel faeces and the L2 larval stage is taken up by copepods. The larva moults to the L3 stage, which is infective for the eel (De Charleroy et al., 1990). Optional paratenic fish hosts can feed on infected copepods and transmit the parasite to eels (Moravec & Skorikova, 1998; Thomas & Ollevier, 1992). (**B**) Photograph of *A. crassus* adults recovered from a dissected swim bladder.

the effects of the second stressor. Second, the two stressors do not influence each other in a way that their combined effect is additive and, third, there can be an interaction between the stressors that is either synergistic or antagonistic (Birk et al., 2020). In addition, there can be special cases, for example the reversal of the response to combined stressors compared with the predicted effect (Jackson et al., 2016; Vos et al., 2023).

In the present study, we summarized examples that illustrate the combined effects of parasites and pollutants on the response of the host, focusing on aquatic parasites. Examples that refer to the mere effects of the parasite are not considered here. Also, we are not addressing studies describing the effects of stressors on the parasite population or community. Furthermore, we want to highlight some fields of research that should be addressed to improve our understanding of the role of parasites in ecotoxicological research. Overall, we intend to create awareness in the ecotoxicology community for the wide variety of effects parasites might have alone or in combination with other stressors on the physiological homeostasis of their hosts in field and experimental studies. Moreover, when addressing regulatory issues with the aim of determining safe environmental contaminant concentrations, such approaches should also consider parasitised test organisms because

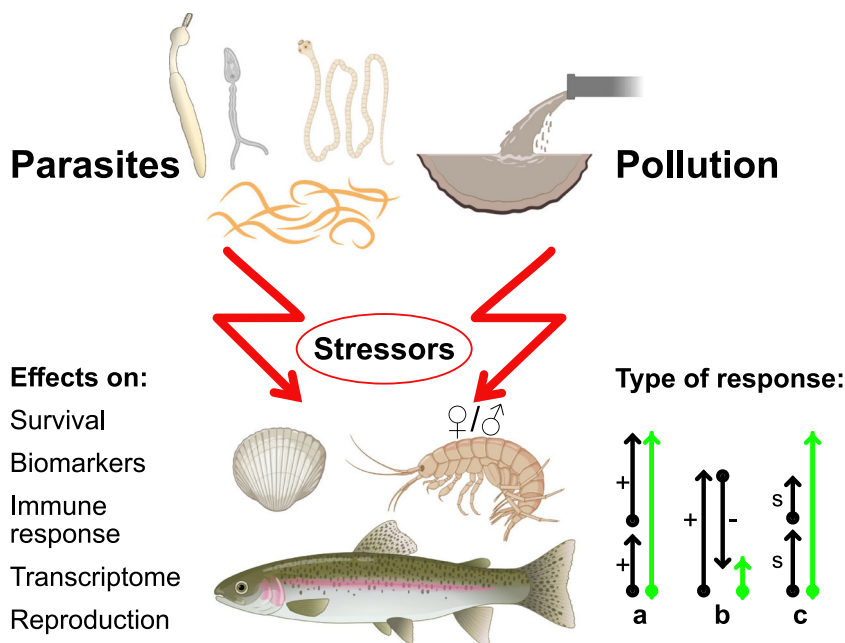**FIGURE 5:** Schematic overview of the effects of parasitism and pollution-related stress on organisms at various levels. Potential response is shown: (a) additive effect of both stressors, (b) antagonistic effect, and (c) synergistic effect. Black arrows, effect of individual stressor; green arrows, combined effect of both stressors; +/− indicates direction of effect). Some elements of the figure were created with BioRender.com.

parasites could alter both contaminant accumulation patterns and host responses to contaminants.

COMBINED EFFECTS OF PARASITES AND OTHER STRESSORS

In this section, we give examples of the response of organisms to both parasites and other (mostly chemical) stressors. The examples are grouped by the way of stressor interactions (additive, synergistic, antagonistic) as far as this can be inferred from the results. Finally, we will address several further aspects that determine the interaction of parasites and other stressors.

Putative additive effects

An additive effect occurs if the measured response of a test organism to a chemical stressor is further increased due to infection by a parasite. There are not many examples that could be recovered from the literature describing an additive effect of parasite + stressor. This might indicate that the interaction of parasites and additional stressors shows a more complex pattern in most cases. One example of a significant additive effect on mortality was found for sockeye salmon (*Oncorhynchus nerka*) that were exposed to zinc if in addition they were infected with adult cestodes (*Eubothrium salvelini*). The time to reach 50% mortality was reduced by 25% in infected and exposed fish relative to uninfected and exposed fish (Boyce & Yamada, 1977). Similarly, individuals of three-spined sticklebacks (*Gasterosteus aculeatus*) infected with plerocercoid larvae of the cestode *Schistocephalus solidus* showed increased mortality (maximum reduction of mean period of survival from ~800 to 300 h) and consequently a lower 50% lethal concentration (LC50) for cadmium compared with uninfected fish (Pascoe & Cram, 1977). On the sublethal level, an additive effect of parasite and pollution on the number of pigmented macrophages was observed in spottail shiners (*Notropis hudsonius*) infected by the apicomplexan *Eimeria degiustii* (Thilakaratne et al., 2007). Additive effects were also detected for ectoparasites and pollution exposure. In the guppy *Poecila reticulata*, exposure to zinc led to increased epidermal thickness, and infection with the monogenean *Gyrodactylus turnbulli* further increased this effect at moderate parasite densities (Gheorghiu et al., 2012). A similar additive effect was found for the activities of the biomarkers aspartate aminotransferase and alanine aminotransferase, and the concentrations of creatinine and urea in fish (*Oreochromis niloticus*, *Clarias gariepinus*) exposed to elevated metal levels and ectoparasites (Monogenea, Crustacea, Protozoa). The biomarker levels in infected fish were increased by 13% to 40% compared with uninfected fish (El-Seify et al., 2011).

These examples show that the lack of consideration of parasite infections can lead to an overestimation of the toxicity of a pollutant according to the effects on the host. On the other hand, results obtained from parasite-free populations can lead to false conclusions about the toxic potential of a substance under field conditions when parasites come into play.

Putative synergistic effects

In contrast to the simple additive effect of two stressors, synergistic effects might lead to unexpected results that cannot be predicted based on the single stressor effects. In some cases, the effects of toxicants only become detectable in parasitized hosts (Coors & De Meester, 2008; Coors et al., 2008; Rothe et al., 2022). Furthermore, toxicant effects can be increased by the parasite to a higher level than expected based on the outcome of each single stressor exposure (either pollution or parasite) due to a synergistic effect of the two stressors (Thilakaratne et al., 2007). As a consequence, the combined effect of parasites and pollution is higher than the sum of the two effects measured in a single exposure, thus parasites can make pollution effects detectable, which may result in a pollutant being deemed environmentally relevant. Conversely, the effects of parasites can become apparent through additional exposure of the host to further stressors. For example, a differential response of the biomarker lipid peroxidation (~26% higher in infected fish) between individuals of yellow perch (*Perca flavescens*) that were infected or uninfected with the nematode *Raphidascaris acus* was only observed if an additional chemical stressor was present (Marcogliese, Brambilla, et al., 2005). A comparable reaction was found in female *Gammarus roeselii* that were exposed to cadmium and infected with microsporidian parasites. The amphipods showed reduced energy reserves (~40% decrease in total lipids and 30% decrease in glycogen level relative to the uninfected amphipods), elevated susceptibility to oxidative stress (up to 60% decreased levels of reduced glutathione relative to uninfected amphipods) and approximately 50% increased cellular damage (based on levels of malondialdehyde) compared with uninfected cadmium-exposed individuals. Parasite infection alone did not affect the tested biomarkers (Gismondi et al., 2012b). Presumably, the change in host metabolism caused by the parasite leads to a stronger response to another stressor. This in turn illustrates that a parasitized population may already show effects at lower pollutant concentrations than would be the case with a non-parasitized population.

Putative antagonistic effects

In some cases, parasites increase the tolerance of the host to stressors due to an antagonistic effect of the parasite. In this context, Piscart et al. (2007) found that acanthocephalan-infected amphipods show an increased tolerance to elevated salinity levels of approximatley 60% to more than 100% based on LC50. Similarly, cestode larvae were described to increase *Artemia* sp. resistance to arsenic during acute toxicity tests (Sánchez et al., 2016). In infected *Artemia* sp., consistently increased LC50 values (50% to over 100%) were found compared with uninfected conspecifics. Even after increasing the water temperature from 25 °C to 29 °C the beneficial effects of the cestode infection prevail with infected *Artemia* sp. The latter showed approximately 60% higher levels of catalase and approximately 50% higher glutathione reductase activity compared with uninfected individuals, which both can be

interpreted as protection measures against (temperature-induced) oxidative stress (Sánchez et al., 2016).

Likewise, a positive effect on survival of infected compared with uninfected hosts was found in some cases for trematode-infected snails (*Zeacumantus subcarinatus*) that were exposed experimentally to different ocean-acidification conditions. At pH 7.6, mortality ranged between 3% and 23% in infected snails (depending on the trematode species) and was 28% in uninfected snails. At pH 7.4, the mortality rate of infected snails ranged from 13% to 31% compared with 22% for the uninfected snails. In contrast at pH 8.1, the mortality rate of uninfected snails was lower (3%) compared with infected snails (7%–33%; MacLeod & Poulin, 2016b). A similar finding was made for trematode-infected mussels (*Pisidium amnicum*) exposed to pentacholorophenol. The mean survival time of the infected mussels was increased by more than 100% at 19 °C but there was an overall negative fitness effect of the parasite due to castration of the host (Heinonen et al., 2001). Reduced mortality of the host even under stressor exposure might be beneficial for the parasite because the host will provide habitat and resources for growth, development, and/or multiplication of the parasite (e.g., trematode larvae in snails). Even for trophically transmitted parasites (e.g., cestode larvae in *Artemia* sp.) survival of the intermediate host is essential during the development of the parasite larva (until it is infective for the next host; see Bailly et al., 2018; Dianne et al., 2011; Franceschi et al., 2008). Furthermore, host death might interfere with transmission if the final host feeds only on live prey.

Another example of a potential protective effect of acanthocephalans was found in chub (*Squalius cephalus*), where significantly lower oxidative damage was observed in tissues of chub that were exposed to organic pollutants if they were also infected with acanthocephalans (*Pomphorhynchus* sp.; Molbert et al., 2020). In general, some acanthocephalan species are presumably beneficial for their host because there are several studies showing the accumulation potential of acanthocephalans for metals. Tissue concentrations of metals in the parasite can highly exceed those of the host and metal concentrations can even be reduced in tissues of infected compared with uninfected hosts (Sures, 2006; Sures, Nachev, Selbach, et al., 2017; Sures et al., 2023).

Antagonistic effects of parasites can also have negative consequences for the host if a protective stressor response (e.g., hsp70, metallothioneins) is decreased in infected hosts. Such a case was found in cockles (*Cerastoderma edule*) infected by trematodes and exposed to cadmium. By reducing the production of protective metallothioneins by 70% relative to the uninfected hosts, the parasites impaired the detoxification mechanisms of the host and caused an increase in cadmium accumulation (795 ng/g in infected vs. 569 ng/g in uninfected cockles) and presumably increased toxic effects (Baudrimont & de Montaudouin, 2007). The larvae of the acanthocephalan parasite *Polymorphus minutus* reduced (~80% compared with uninfected amphipods) or completely disrupted the hsp70 response caused by cadmium or heat exposure in amphipods (*Gammarus fossarum* and *G. roeselii*; Frank et al., 2013; Sures & Radszuweit, 2007). It is not clear to

date whether the reduction of the detoxification capabilities or the cellular defence mechanisms have an effect on host fitness. Also, the potential biological significance of the impairment for the parasite is not known.

Another presumably antagonistic effect of the combination of parasite and chemical stress was observed in a study of European eel (*Anguilla anguilla*) infected with the swim-bladder nematode *Anguillicola crassus* that were exposed to both cadmium and 3,3′,4,4′,5-pentachlorobiphenyl (PCB 126). At the end of the experiment, cortisol levels in the parasite-infected and chemical-exposed group were only 60% of those of the parasitized eel without exposure. An explanation could be cortisol-mediated immune suppression induced by the parasite that might be disturbed by the chemical exposure (Sures et al., 2006). However, it is not known whether the interference with immune suppressive mechanisms of the parasite influences the host defence against the parasite.

No combined stressor effects

It is important to note that parasites do not necessarily have an influence on the effects of further stressors in the host. For example, no effect of parasitism on the host response was found in toxaphene-exposed Arctic charr (*Salvelinus alpinus*) infected with the tapeworm *Diphyllobothrium dendriticum* and tadpoles of the frog *Rana palustris* exposed to malathion and infected with the trematode *Echinostoma trivolvis* (Blanar et al., 2005; Budischak et al., 2009). Similarly, parasites had no significant effect on the biomarker response of common carp (*Cyprinus carpio*) and African sharptooth catfish (*Clarias gariepinus*) sampled from stream sites with elevated metal concentrations in the study of Erasmus et al. (2020), even though several metals were accumulated by the parasites and thereby reduced in the host tissues. These examples show that it is not possible to assume in all cases that parasites will affect the response of the host to pollutants. Nevertheless, the host stress response in relation to parasites can be affected by further factors, for example the infection intensity of the parasite (see section *Additional factors influencing the host stress response*).

Additional factors influencing the host stress response

The effect of parasites on the host response to other stressors is difficult to generalize because the outcome can be dependent on a variety of factors, some of which are outlined in this section.

Temperature. When using temperature as a stressor it was found that infection by the trematode *Himasthla elongata* increased the mortality of the gastropod host *Littorina littorea* at elevated temperatures (e.g., median survival duration of 5 and 16 days for infected and uninfected snails, respectively; Diaz-Morales et al., 2022). In a similar way, brown trout (*Salmo trutta*) fry and alevins exposed to the oomycete *Saprolegnia parasitica*

showed increased mortality in the parasite treatment (50% up to 100% mortality compared with <30% in the uninfected fish) when facing intermittent temperature increases (Casas-Mulet et al., 2021). Temperature is normally controlled in laboratory experiments and reported in field studies. However, when planning studies, especially with parasites, it must be considered that different temperature levels can lead to significantly different results. There are several other examples where biomarker responses due to parasites and additional stressors showed additive, but overall complex patterns (e.g., contrasting results depending on host sex). These studies will be shown in the following sections.

Species-specific effects. Effects of stressors were found to be highly species-specific depending on the parasite and host species studied, with clear differences found even for closely related taxa. For example, exposure to desethylatrazine caused an increase in mortality in the freshwater gastropod *Stagnicola elodes* if infected by a trematode (gymnocephalus-type cercariae, ~30% survival) but did not affect mortality in exposed snails infected with *Echinoparyphium* sp. (~80% survival; Koprivnikar & Walker, 2011). Parasite species also made a considerable difference in the study of MacLeod and Poulin (2016a), who found significantly variable rates of oxygen consumption and tissue glucose levels in the intertidal gastropod *Z. subcarinatus* kept at different pH treatments depending on the trematode species present. Similarly, the reaction of the stress protein hsp70 can be modulated by parasites, but the outcome depends largely on the host–parasite system studied. While elevated temperature or cadmium exposure in combination with microsporidian infection caused increased hsp70 levels in *Gammarus pulex* and *G. fossarum*, there was no modulation of hsp70 by the acanthocephalan *P. minutus* in *G. fossarum*, irrespective of the exposure (Chen et al., 2015; Grabner et al., 2014). On the other hand, an over 2000% higher induction of hsp70 was found in the study of Frank et al. (2013) in *P. minutus*-infected *G. fossarum*. In the same study, cadmium exposure also induced a more than 7000% increase of hsp70 levels, whereas the combination of parasite and cadmium resulted in a lower hsp70 response than the metal exposure in uninfected individuals (Frank et al., 2013). These partly contradictory results might be due to unnoticed microsporidian infections in the amphipods in the study of Frank et al. (2013). Rothe et al. (2022) found an increasing effect on several biomarkers in the same *P. minutus*–*G. fossarum* system, whereas there was no significant effect of treated wastewater. Interestingly, the same acanthocephalan species completely disrupted the hsp70 response of the amphipod *G. roeselii* even after exposure to palladium and heat (Sures & Radszuweit, 2007). The impairment of the stress response by one parasite-pollutant combination can be further modulated by coinfecting parasites present in the same host individual. For example, microsporidian parasites can disrupt the effects of acanthocephalan parasites on the host. In *G. roeselii* infected with both the microsporidian *Dictyocoela roeselum* and the acanthocephalan *P. minutus*, the microsporidian effects on the biomarker response dominated that of the acanthocephalan compared with infections with only a single parasite (Gismondi

et al., 2012a). The reason for this observation might be the more severe impact of the microsporidians on host metabolism during phases of massive multiplication.

These examples make it clear that it is not appropriate to speak of parasites in general terms if we want to understand ecotoxicological relationships. On the contrary, different parasite taxa need to be considered individually and their impact on the host has to be assessed in each case.

Concentration-dependent or parasite infection intensity effects. It was found that the effects of parasites can vary greatly depending on the concentration of the pollutants or the number of parasite stages per host. For example, trematodes in fish (yellow perch, *P. flavescens*) caused an increase in catalase and a decrease of glutathione reductase activity but only at sites with the highest pollutant levels, while no parasite effect on the biomarker response was observed in fish from sites with low pollutant concentrations (Marcogliese et al., 2010). Molbert et al. (2021) also found a response of chub (*S. cephalus*) parasitized with acanthocephalans (*Pomphorhynchus* sp.) depending on the exposure levels to polycyclic aromatic hydrocarbons (PAHs). Interestingly, levels of oxidative stress were more than 60% higher in parasitized fish exposed to low PAH levels but approximately 40% lower at higher PAH concentrations compared with uninfected fish from the same exposure. Similarly, northern leopard frogs (*Lithobates pipiens*) naturally exposed to different atrazine levels showed an interaction of the nematode parasite *Oswaldocruzia* sp. and atrazine on the oxidative stress marker thiol. Thiol levels were increased with parasite abundance, but only at low atrazine levels while decreasing thiol levels were measured with increasing parasite abundance at high atrazine levels (Marcogliese et al., 2021). An effect of infection intensity was found in yellow perch (*P. flavescens*) infected with trematode metacercariae of the trematode *A. brevis*. If more than 10 metacercariae were detected, the fish showed 40% to 50% higher levels of lipid peroxidation than fish with <10 metacercariae (Marcogliese, Brambilla, et al., 2005).

Overall, these results show that the stress response of the host often is not linearly related to parasite intensity and/or pollutant concentrations, therefore it is important to test a range of pollutants, but at the same time to consider parasite infection intensity for the effect that is caused in the host. Infection intensity is not always considered, mainly for microparasites that cannot be quantified easily. For parasite stages that are not directly countable, semiquantitative methods could be applied (e.g., rating intensity from low, medium to high), or molecular methods such as quantitative polymerase chain reaction could be used.

Effect of host age. The age distribution in the host population plays an important role to determine infection parameters and disease progression (Ben-Ami, 2019; Thomas, 2002). This aspect has been rarely investigated in an ecotoxicological context. For example, Thilakaratne et al. (2007) found stronger parasite-induced effects according to the biomarker response in younger spottail shiners (*N. hudsonius*) compared with older

fish. In many cases it will be difficult to determine the age of the hosts if no laboratory-bred individuals are available. Host size can be used for some species for an approximation of host age or at least to distinguish juvenile from adult individuals.

Effect of host gender. Gender is also an important factor that can have a tremendous effect on the outcome of eco-toxicological studies, as has been shown, for example, for amphipods (Gismondi et al., 2013). Accordingly, the response to the combined effects of parasites and further stressors is often dependent on the host sex. Minguez et al. (2009) found structural changes in the lysosomal system and an increase in neutral lipids in the tissues of male *Dreissena polymorpha* infected with parasites and exposed to pollution (30% higher males), whereas the opposite trend was found in parasitized and exposed female *D. polymorpha* (45% higher in females). In an amphipod–acanthocephalan system, under cadmium exposures, decreased mortality was found for *G. roeselii* males infected with *P. minutus* compared with uninfected amphipods (LC50 almost 200% higher in infected amphipods). In contrast, mortality was increased (LC50 more than 200% higher in uninfected amphipods), and a stronger response of toxic effect biomarkers was found in infected and exposed females compared with uninfected individuals (e.g., 50% increased malondialdehyde levels in cadmium-exposed uninfected females, whereas infected females showed an increase of 160% under cadmium exposure; Gismondi, Beisel, et al., 2012; Gismondi, Cossu-Leguille, et al., 2012). Similarly, glycogen levels were increased by 60% only in female *G. fossarum* infected with the microsporidian *Dictyocoela duebenum* and exposed to sublethal cadmium levels, but not in males, in the study of Chen et al. (2015). Complex sex-specific differences were also found in the marine amphipod *Gammarus tigrinus* exposed to different temperature levels and infected with the trematode *Podocotyle atomon*. Infected females showed lower phenoloxidase activity than males at 14 and 18 °C, and catalase activity was increased at higher temperatures for infected males and uninfected females while being increased at lower temperatures for infected females (Diaz-Morales et al., 2023).

These results highlight that host sex should be used as a factor in the analysis of stressor effects. Furthermore, it is important to improve the understanding of differences in the reaction of female and male individuals to pollutants and parasites, and to clarify the underlying mechanisms.

FUTURE DIRCTIONS OF RESEARCH ON PARASITES AND STRESSORS

The examples presented in the previous section (*Combined effects of parasites and other stressors*) illustrate the influence of parasites on the stress response of the host and therefore their importance for ecotoxicological studies. We therefore advocate the deliberate inclusion of parasite infection in the planning and design of ecotoxicological studies. The possible forms of interaction of the effects (additive,

synergistic, antagonistic) should be taken into account when formulating hypotheses. Furthermore, based on the additional factors influencing parasite/stressor interactions outlined above, we recommend that the following factors, which have received little attention to date, should be considered to a greater extent. First, different temperature and pollutant levels should be applied to study the gradient of responses of both parasitized and unparasitized hosts. If possible, parasite infection intensities should be assessed, or even controlled. Second, host age and gender should be assessed and used as factors whenever possible. This will improve the systematic investigation of parasite effects, including additional stressors, and lead to a mechanistic understanding of how parasites influence the host response.

Furthermore, there are some elements of the host biology that can be influenced both by environmental stressors and parasites, but their interaction is only poorly understood: endocrine effects of parasites and pollutants, and the interactive effects of parasites and chemical stressors on the host microbiome. Due to their importance for ecotoxicological questions, both aspects will be summarized briefly in the following sections. In addition, there are common test organisms that have not been subject to studies involving parasites, although they can be affected by various parasites in natural systems.

Effects of parasites on the endocrine system of the host

Some parasites interfere with the endocrine system of their host, mostly impairing the reproductive system or causing the phenomenon of intersex, for example the cestode larva of *Ligula intestinalis* in fish, trematodes in snails, or vertically transmitted (from mother to offspring) microsporidians (Ford & Fernandes, 2005; Grabner & Sures, 2019; Jobling & Tyler, 2003; Lewis et al., 2015; Morley, 2006; Trubiroha et al., 2009). Pollution might have similar effects that can be difficult to disentangle from the parasite (Ford et al., 2006; Schabuss et al., 2005; Yang et al., 2008). For example, in the amphipod *G. pulex* it was found that vertically transmitted microsporidian parasites interfere with the effects of the endocrine disruptor cyproterone on sperm production of the host (Gismondi et al., 2017).

Further studies are needed to understand the combined effect on the endocrine system of parasites and chemicals, for example those enhancing the knowledge of relevant biomarkers to assess feminization or sexual dysfunction and distinguish between the effects of parasites and toxicant exposure (Short et al., 2014). As a starting point, relatively well-studied endocrine-disrupting parasites, for example *L. intestinalis* as a model parasite in vertebrates and microsporidians in amphipods for invertebrates, should be studied in more detail. However, for the latter, much more fundamental knowledge needs to be gained on the endocrine-disrupting effects of the parasite itself. The goal should be to analyse the combination of parasites that affect the hormone system of the host with exposure to endocrine-disrupting chemicals.

Effects of the host microbiome

Studying the role of the microbiome of organisms is becoming more and more important in various research fields. This applies also to ecotoxicology, where the interplay of the gut microbiota, toxicant exposure, and physiological effects is being investigated (Claus et al., 2016). Recent findings highlight that parasites have a substantial influence on the host microbiome (Dheilly et al., 2019; Fu et al., 2022) and that the effects of parasites on the gut microbiota of fish (chub, *Squalius cephalus*) can be more pronounced than exposure to PAHs (Colin et al., 2022). Nevertheless, this research field is in its infancy and the significance of changes in the microbiome (e.g., by parasites and/or pollutants) for the host is still unknown, therefore the first step is to improve knowledge of the microbiome function in vertebrates and invertebrates. The second step is to test of the microbiome response to parasite and pollutant exposure. Exposure-related changes in the host microbiome might also provide explanations for stressor effects reported previously (e.g., biomarker responses).

Further parasites and pathogens that might have an influence on the stress response

The parasites of some commonly used test organisms have been well characterized and we already have some knowledge of the combined effects of toxicant exposure, for example for amphipods, fish, snails, and mussels (see above). *Daphnia* spp. can be affected by a number of parasites under natural conditions (Stirnadel & Ebert, 1997) and provide a great opportunity to study parasite (e.g., Microsporidia) and environmental stressor effects under laboratory conditions because protocols exist for the controlled infection of *Daphnia* under these conditions (e.g., Coors et al., 2008). However, there is a number of common ecotoxicological test organisms for which only limited information is available on the role of parasites in addition to other stressors. Zebrafish, for example, can be affected by several parasite taxa even under laboratory conditions (Kent et al., 2020) and infections by microsporidians were even found in research strains with sometimes subclinical infections that might affect the outcome of experiments (Sanders et al., 2012). Among invertebrate models, the nematode *Caenorhabditis elegans* is used in ecotoxicological standard tests (e.g., Schertzinger et al., 2017), but free-living individuals can be infected by microsporidians or pathogenic bacteria (Hodgkin & Partridge, 2008), therefore toxicity testing including parasitized test groups might be possible for this species. *Lubriculus variegatus* is also commonly used for ecotoxicological sediment testing (e.g., Kontchou et al., 2023), but *Lumbriculus* spp. (and other oligochaetes) are also common hosts for myxozoans (Kent et al., 2001). This might be an interesting host–parasite model because infected individuals can be identified according to the detection of actinospores from infected individuals.

Some of the test organisms are available as pathogen-free cultures, for example *C. elegans*, *Lumbriculus* spp., and *Daphnia* sp., and provide the possibility to study toxicant effects without confounding effects from parasites. However, from an ecotoxicological perspective, conclusions drawn from parasite-free laboratory populations might not reflect the response of natural field populations that are affected by parasites. This is particularly relevant for parameters that are used to determine safety limits of substances like LC50 and lowest or no observed effect concentrations. These values might be considerably different if determined with parasite-free test organisms or if parasite infection is included, therefore including parasites in ecotoxicological studies will provide a more realistic assessment of stressor effects in a natural environment. Such experiments, in which parasite infection is controlled, are less problematic if an infection can be detected easily, such as for acanthocephalan cystacanth larvae in amphipods that can be observed in the living host, and host individuals can be selected according to the experimental design (Grabner & Sures, 2019). Nevertheless, most parasites are visible only after the dissection of the host and the use of further diagnostic techniques such as molecular detection. In the latter case, initial parasitological screening of field populations will help to estimate the prevalence of parasites in the population and help in planning experiments. Test organisms should then be analysed for parasites at the end of the experiment to be able to elucidate potential parasite effects on the selected endpoints. Alternatively, experimental infections of laboratory-cultured test organisms can be conducted in the course of ecotoxicological experiments if appropriate protocols for a standardized infection are developed.

In addition to protist or metazoan parasites, there are several pathogens such as viruses and bacteria that rarely have been considered as an influencing factor in ecotoxicological studies because their impact on the host is often not known (for amphipods, see Bojko & Ovcharenko, 2019; for *Daphnia,* see Stirnadel & Ebert, 1997). Those pathogens and further, undescribed parasites have to be characterized in more detail to know the full "inventory" of the test organisms.

CONCLUSION

If we want to understand ecosystem processes, including the effects of toxic substances on organisms and populations, we need to consider parasites as integral parts of ecosystems to get a reliable estimation of pollutant effects under real-life conditions and to determine the safety limits of chemicals that reflect the responses of natural populations. We therefore should consider naturally occurring parasites when using test organisms from the field and, if possible, also conduct tests with laboratory-infected hosts in addition to other stressors.

Conflict of Interest—The authors declare no conflict of interest.

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