Effects of multiple stressors in fish: how parasites and contaminants interact

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Abstract

Interest in local environmental conditions and the occurrence and behaviour of parasites has increased over the last 3 decades, leading to the discipline of Environmental Parasitology. The aim of this discipline is to investigate how anthropogenically altered environmental factors influence the occurrence of parasites and how the combined effects of pollutants and parasites affect the health of their hosts. Accordingly, in this paper, we provide an overview of the direct and indirect effects of pollutants on the occurrence and distribution of fish parasites. However, based on current knowledge, it is difficult to draw general conclusions about these interdependencies, as the effects of pollutants on free-living (larval) parasite stages, as well as their effects on ectoparasites, depend on the pollutant–host–parasite combination as well as on other environmental factors that can modulate the harmful effects of pollutants. Furthermore, the question of the combined effects of the simultaneous occurrence of parasites and pollutants on the physiology and health of the fish hosts is of interest. For this purpose, we differentiate between the dominance effects of individual stressors over other, additive or synergistically reinforcing effects as well as combined antagonistic effects. For the latter, there are only very few studies, most of which were also carried out on invertebrates, so that this field of research presents itself as very promising for future investigations.

Introduction

Aquatic organisms, and fish in particular, are affected by a variety of stressors caused by anthropogenic influences that lead to changes in environmental parameters. These in turn elicit stress responses of the organism in the sense that the affected organisms show reactions outside their normal range. Stressors include chemical pollutants (i.e. contaminants), nutrients, flow velocity, pH, dissolved oxygen, disturbance in light and temperature regimes and many other physico-chemical variables that can be significantly altered by anthropogenic activities (e.g. Birk et al., 2020). In this paper, the focus is mainly on the chemical pollutants that can cause acute and/or chronic effects in biota when exceeding aqueous concentrations above their natural range of occurrence. However, other factors such as the temperature regime, pH and dissolved oxygen are also considered, as they may influence the solubility and bioavailability of pollutants or, conversely, the pollutants may influence the natural ranges of some of these factors (e.g. oxygen content, pH) and thus contribute significantly to the effects of the pollutants.

Chemical contaminants include various micropollutants of inorganic and organic nature, organometallic compounds, but also dissolved salts (e.g. salinization) and nutrients (e.g. NO$_3^-$, NO$_2^-$, NH$_4^+$, PO$_4^{3-}$). The inorganic pollutants comprise various trace elements (metals and metalloids such as Cd, Pb, As), which may be of geogenic origin (Erasmus et al., 2022). In most cases, however, the elevated concentrations are related to anthropogenic activities such as mining, industrial and domestic wastewater, agriculture, erosion of landfills, waste dump and many others (e.g. Schertzinger et al., 2018, 2019; Kontchou et al., 2021; Rothe et al., 2022; Erasmus et al., 2022). Metals can affect for example the embryonic and larval development of fish, its growth and fitness as well as reproduction (e.g. summarized in Taslima et al., 2022). The modes of action comprise effects on molecular and cellular levels as well as on the immune system, on the physiology, and the metabolism of fish (see Taslima et al., 2022 and references therein). Some metals such as Cd, Cr, Hg and Pb may also act as endocrine disruptors (reviewed in Chakraborty, 2021).

Elevated levels of dissolved salts (e.g. salinization) and nutrients are also related to anthropogenic activities and can directly affect fish or indirectly affect environmental conditions (e.g. in the case of eutrophication) and the species composition of the biota (Schröder et al., 2015) as well as food availability for fish in general. Organic pollutants include a large group of compounds used in industry (e.g. PCBs, PAHs, plasticizers, flame retardants) and agriculture (e.g. pesticides), but also some that are used as pharmaceuticals or personal care products or enter domestic wastewater as metabolic end products. Similar to inorganic pollutants, they can have effects on different levels of organization in fish and might additionally act as endocrine disruptors (Tierney et al., 2013). In addition to the pollutants mentioned, parasites might represent an additional stressor for fish at the individual, population or community level. Parasite infections can reduce host

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fitness by inducing different pathological, immunological and physiological responses (e.g. Sures et al., 2001; Munderle et al., 2004; Buchmann and Bresciani, 2006; Gerard et al., 2016). Nutrition and energy drain as well as host manipulation can reduce the performance and fitness of infected individuals. Parasite infection can also negatively affect the dynamics and density of fish populations and thus the entire fish community. Population effects are particularly significant for infections with parasites that cause severe pathological damage (e.g. Sokolowski and Dove, 2006; Shafaquat et al., 2016; Barisic et al., 2018; Dezfuli et al., 2021) or with parasites that act as endocrine disruptors and parasitic castrators (e.g. Trubiroha et al., 2010, 2011) and/or manipulate their host to make it more vulnerable to predation (e.g. Giles, 1983; Museth, 2001; Gabagambi et al., 2019; Svensson et al., 2022).

In general, parasite infections increase the susceptibility of their hosts to various stressors (Combes, 1995), so that infected fish exposed to multiple stressors may react differently than uninfected conspecifics. The aim of this paper is therefore to summarize and discuss what is known about the complex interactions between parasites and various contaminants from the perspective of the fish host (see Fig. 1). In terms of Environmental Parasitology, this overview sheds light on the role of parasites in ecosystems where multiple stressors interact. First, we provide an overview of (i) the direct interaction between parasite stages which are in close contact to environmental contaminants (i.e. ectoparasites and free-living stages of endoparasites), before (ii) summarizing indirect effects of pollutants on fish parasite occurrence and distribution. Additionally, we give examples of (iii) the complex fish–parasite–pollution interaction and finally, provide some (iv) concluding remarks and an outlook for future research.

**Direct interaction between parasites and contaminants in the aquatic environment**

Parasites constitute a significant part of natural ecosystems and produce a considerable amount of their biomass (Kuris et al., 2008; Soldanová et al., 2016). Similar to free-living organisms, parasites are affected by and respond to environmental conditions. Fluctuations in the population dynamics of parasites are still not very well understood, but in several cases, the reasons lie in changes in environmental conditions (pollution, anthropogenic impact, etc.; see Thieltges et al., 2008) as well as in invasive species encountering susceptible hosts after their arrival and then succeeding accordingly (Goedknegt et al., 2016). Over the last 2 decades, research has shown that environmental factors have a significant impact on parasites and can directly influence the composition and diversity of parasite communities. The direct mode of action includes effects on adult ectoparasites or larval stages that are in immediate contact with the environment (Gheorgiu et al., 2006; Gheorghiu et al., 2007; Thieltges et al., 2008; Sures et al., 2017). Pollution-induced lethal responses lead to lower transmission efficiency of parasites, which in turn affects the structure and dynamics of parasite populations. Moreover, ectoparasites have been found to respond very sensitive to pollution (e.g. eutrophication or chemical pollution) (Gilbert and Avenant-Oldewage, 2021) similar to endoparasites with free-living larval stages (e.g. cercariae, miracidia), which may also be directly affected by environmental conditions (summarized by Thieltges et al., 2008). A meta-analysis of published data (Gilbert and Avenant-Oldewage, 2021) has shown that pollution can have both positive and negative effects on monogenean communities, while some pollutants show no clear effects. It can be seen that metals tend to have a negative effect on monogenean communities (lower abundance of some species and lower diversity), while eutrophication has a positive effect (see Gilbert and Avenant-Oldewage, 2021 and references therein). Direct effects of pollutants on endoparasites are due to exposure of free-living larval stages to pollutants. Metals have been reported to affect trematode transmission by reducing the longevity, viability and infectivity of cercariae (Pietrock and Marcogliese, 2003; Morley et al., 2006). Similar effects were reported for organic pollutants such as various pesticides (e.g. Koprivnikar et al., 2006, 2007; Rohr et al., 2008; Raffel et al., 2009; Hua et al., 2016).

Free-living stages of endoparasites and ectoparasites can not only be affected by pollutants, but also should in turn be able to influence the level of pollutants in the environment. For example, cercariae, which are excreted in large numbers and
biomass by the mollusc intermediate host (Soldánová et al., 2016; Díaz-Morales et al., 2022), could act as a pollutant sink at low spatial scales, influencing the distribution and further bioavailability of chemicals when accumulated by them. During their short lifespan, cercariae provide a food source for various aquatic organisms (Johnson et al., 2010), including fish, and thus may additionally contribute to the distribution and location of chemicals within the various components of food webs. It can be assumed that a significant proportion of pollutants could be stored in free-living stages of parasites in ecosystems, as various parasitic taxa have an excellent accumulation capacity (see e.g. Sures et al., 2017). Interestingly, to the best of our knowledge, no study is available addressing a possible pollutant uptake by cercariae although studies by Morley and colleagues (Morley et al., 2003, 2006) suggest the availability of metals for cercariae with subsequent fatal effects. Regardless of a possible pollutant load, the majority of the cercariae die, sediment together with the suspended matter and become demineralized. Ectoparasites such as crustaceans and monogeneans, which can accumulate metals (Pérez-del-Olmo et al., 2019; Nachev et al., 2022), can also presumably take up pollutants from the environment. It has already been shown that, for example, metals may become incorporated into the scleritized structures of the haptor in monogeneans (Gilbert and Avenant-Oldewage, 2017). Often, such a contaminant exposure lead to malformation of the haptor in several families of monogeneans (see e.g. Šebelová et al., 2002; Pečinková et al., 2005; Dzika et al., 2007; Rodríguez-González et al., 2020) and could therefore even be used to indicate metal pollution in aquatic ecosystems (Gilbert and Avenant-Oldewage, 2021).

**Indirect effects of contaminants on parasite occurrence and distribution in the aquatic environment**

Indirect effects of contaminants on individual parasites and their communities refer to the presence and abundance of free-living intermediate or definitive hosts involved in the life cycle of multi-host parasites. Host organisms require an optimal range of environmental conditions and respond to deviations from these or to the presence of stressors with reduced abundance, while in the extreme range of conditions they may even be absent. As a result, parasites show lower species richness and diversity, and changes in species composition. Nachev and Sures (2009) reported lower parasite diversity in fish from polluted sites (higher metal concentrations and eutrophication) in comparison to less polluted localities. Similar patterns were reported by Krause et al. (2010) in relation to general water quality in combination with adverse environmental conditions as well as by Barišić et al. (2018) and Braicovich et al. (2020) as a consequence of industrial and agricultural activities and effluent of a wastewater treatment plant. The richness and structure of parasite communities were found to follow gradients of salinity and eutrophication, with fecal coliform counts and temperature serving as proxies for the pulp mill and effluents (Blanar et al., 2011), land use and the concentration of hydrocarbons (PAHs) in sediments (Blanar et al., 2016), pharmaceuticals (Pravdová et al., 2022) or levels in PCBs in sediments (van Urk et al., 2016), or PCB 126-exposed eels when compared to unexposed conspecifics (Sures and Knopf, 2004). Moreover, a combined Cd- and PCB 126-exposure together with experimental infection with A. crassus induced significantly increased cortisol levels in eel blood, which themselves are assumed to be immunosuppressive (Sures et al., 2006).

**Interactive effects of simultaneously occurring pollution and parasitism on fish**

Following the ecological concept of stressor interaction (Birk et al., 2020) pollutants and parasites can interact in many ways (Fig. 2) and 3 main types of impact on their hosts can be distinguished: (1) only 1 of the 2 stressors has relevant effects on the host, i.e. the effects of 1 stressor outweigh those of the other stressor (stressor dominance); (2) parasites and pollutants act independently in a way that their joint effect is the sum of the individual effects (additive effects); and (3) 1 stressor either strengthens (synergistic) or weakens (antagonistic) the effect of the other. As previously mentioned various organic and inorganic contaminants can act as toxic substances with adverse effects on the physiology of the host that can be modulated by simultaneously occurring parasites.

In the case of a dominant stressor, there are examples of both parasites as well as pollutants. Especially monoxenous parasites with short life cycles and high infectivity can quickly threaten fish to such an extent that they die, so that further stressors such as pollutants hardly play a role in these scenarios. For example, the monogenean Gyrodactylus salaris has shown high virulence towards East Atlantic salmon in rivers in Norway, leading to high mortality of fry and parr (Heinecke et al., 2007 and references therein). On the other hand, pollutants can also show stressor dominance, especially if they are really highly toxic substances that are present in correspondingly high concentrations. There are a number of environmental disasters that show how dominant and fatal pollution as a stressor can be. One of the most prominent ones in freshwater ecosystems is probably the Sandoz accident that occurred in 1986 in Switzerland (Van Urk et al., 1993). A fire in a chemical production plant led to the release of toxic agrochemicals into the River Rhine, killing a large part of the eel population and severely damaging other fish species and macroinvertebrates as far downstream as the Netherlands (Güttinger and Stumm, 1992).

Probably, the most common scenario is where the negative effects of pollutants and parasites are more pronounced when
Fig. 2. Interactive effects of pollutants and parasites on different organization levels of fish. Parasites are an additional stressor for fish that might superimpose the effects of environmental factors, which can lead to various forms of stressor interaction. In addition to frequently observed additive and synergistic negative effects on fish, there are also examples of antagonistic effects where parasite infections appear to be beneficial to infected individuals. Also, dominance effects might occur where 1 stressor outweigh effects of the other stressor. Effects of these stressors often manifest on molecular and subcellular levels but their effects might be seen on the population or even community level.

they occur together, in the sense of an additive or synergistic interaction, than if only a single stressor were present (Fig. 2). Accordingly, in these cases, the damage to the fish is also significantly greater as if only a single stressor occurs (Sures, 2008b). Many studies have shown that acute and chronic effects of chemicals can be exacerbated by parasitism, through lower fish survival (e.g. Boyce and Yamada, 1977; Pascoe and Cram, 1977; Gheorgiu et al., 2006), poorer body condition (e.g. Thilakaratne et al., 2007) and various physiological markers (e.g. Marcogliese and Pietrock, 2011 and references therein; Sures et al., 2017 and references therein). In particular, interest in the interaction between parasites and environmental pollution has increased in recent years in terms of biomarker responses. Currently, it appears that mostly the pathogenicity of parasites can be enhanced when they coexist with pollutants, such that the negative effects induced by pollution are exacerbated by the parasites (Marcogliese et al., 2010; Frank et al., 2013). However, the modulation of pollutant–biomarker responses in organisms by parasites is a phenomenon that is currently not well understood and therefore deserves further investigation (Sures et al., 2017).

The most interesting interactions are antagonistic effects, where the presence of 1 stressor mitigates the negative effects of the other. The ability of some helminth species such as cestodes, acanthocephalans and nematodes to accumulate pollutants in high concentrations is the best-known example in this context. Due to their enormous pollutant (mainly metals) accumulation capacity, these parasites can significantly reduce the levels of accumulated pollutants within the fish body (summarized in Sures et al., 2017). This has been demonstrated in laboratory and field studies for concentrations of various trace elements whose concentrations were reduced in fish infected by acanthocephalans (Sures et al., 1999, 2003; Filipović Marijić et al., 2013, 2014; Brázová et al., 2015; Torres et al., 2015; Leite et al., 2021) and nematodes (Bergey et al., 2002; Hursky and Pietrock, 2015). Similar patterns were reported also for organic pollutants, with acanthocephalan infected fish (Brázová et al., 2012) having significant lower concentrations of PCBs. From a theoretical point of view, one would expect less severe effects if the pollutant concentration in infected hosts is lower than in non-infected hosts. Lower pollutant-related toxicity could also result if alternative physiological pathways are activated by parasites, leading to changes in the host’s pollutant metabolism. However, these reduced pollutant effects must of course be weighed against the pathological effects of parasites. And this assessment must be carried out individually for each host–parasite–pollutant combination, so that we are currently still a long way from understanding antagonistic effects of parasites and pollutants. Beneficial effects of infection with acanthocephalans on the physiology of fish (reduced oxidative damage) were recorded in natural habitats with higher levels of organic micropollutants (Molbert et al., 2020) and in laboratory exposure studies with PAH (Molbert et al., 2021). Also from non-vertebrate hosts antagonistic interactions between pollutants and parasites are known. Freshwater mussels, Pisidium amnicum, partially infected with larvae of digenean trematodes, were exposed to pentachlorophenol (PCP), resulting in a significantly shorter survival time of the uninfected mussels compared to infected conspecifics, which survived up to twice as long (Heinonen et al., 2001). For Artemia parthenogenetica Sánchez et al. (2016) demonstrated a higher host resistance to increasing arsenic concentrations for intermediate hosts infected with different parasite species.

Compared to additive or synergistic interactions of parasites and pollutants, there have been few studies on antagonistic effects where parasites can reduce pollutant effects. Parasite-reduced pollutant concentrations in infected hosts certainly appear beneficial if hosts face increasing levels of pollution, as lower pollutant concentrations are usually associated with less toxic effects. This relationship should be explored in more detail in future studies, with
a clear focus on whether the negative effects of a parasitosis can be outweighed by the potentially positive effects of lower pollutant concentrations. In addressing these aspects, studies should be conducted not only at the individual level but also, if possible, at the population and ecosystem levels.

Conclusions

The interactions between pollutants and parasites presented here show that parasites must be regarded as organisms that are in close mutual exchange with pollutants. This interaction of parasites and pollutants is significant for both – the occurrence of parasites in ecosystems and for the health of their hosts. In environmental studies, parasites need to be taken into account because they can influence the interaction between fish and pollutants and thus the results of the studies in general. Lower accumulation of contaminants in organisms infected with parasites, for example, could make free-living established indicator organisms less reliable for environmental monitoring. On the other hand, contaminants are capable of significantly affecting fish–parasite interactions and parasite transmission, which may lead to an increase or decrease in parasite infestation in fish populations. Systematic studies on the mechanisms of action and the complexity of the interaction between fish and parasites in a polluted environment are largely lacking, so that the basic relationships are often poorly understood. It is known that parasites are also successfully transferred to the next host in polluted environments through host manipulation (e.g. Fenton et al., 2020). However, there is not much research on changes in host behaviour under pollution conditions and how this affects the transmission efficiency of parasites. Acute or chronic toxic effects on e.g. intermediate hosts may weaken them and make them more susceptible to predation by fish, which could be beneficial for trophically transmitted parasites (e.g. Acanthocephala, Cestoda).

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Author’s contributions

BS and MN conceived the structure of this paper. BS led the writing of the paper, MN oversaw the writing and prepared the figures. All authors contributed critically to the draft and approved the final paper.

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Conflicts of interest

The authors declare there are no conflicts of interest.

Ethical standards

Not applicable here.

References

Barišić J, Filipović Marijić V, Mijošek T, Čož-Rakovac R, Dragun Z, Krasničić N, Ivanović D, Kružličov D and Erk M (2018) Evaluation of architectural and histopathological biomarkers in the intestine of brown trout (Salmo trutta Linnaeus, 1758) challenged with environmental pollution. Science of the Total Environment 642, 656–664.

Baruš V, Šimková A, Prokeš M, Peňař M and Vetesiňk L (2012) Heavy metals in two host-parasite systems: tapeworm vs fish. Acta Veterinaria Brno 81, 313–317.

Berger L, Weis JS and Weis P (2002) Mercury uptake by the estuarine species Palaeonema pugio and Fundulus heteroclitus compared with their parasites, Probopyrus pandalicola and Eustrengyliidae sp. Marine Pollution Bulletin 44, 1046–1050.

Birk S, Chapman D, Carvalho L, Spears BM, Andersen HE, Argillier C, Auer S, Baatrup-Pedersen A, Banin L, Beklögå M, Bondar-Kunze E, Borja A, Branco P, Bucak T, Buije AD, Cardoso AC, Raoul-Marie Couture RM, Cremona F, de Zwart D, Feld CK, Ferreira MT, Feuchtmaier H, Gessner MO, Gieswein A, Gloeboom I, Graeber D, Graf W, Gutiérrez–Cánovas C, Hanganu J, Iskun U, Järvinen M, Jeppeos E, Kotamäki N, Kuijper M, Lemm JU, Lu S, Solheim AL, Mische U, Moe SJ, Nóg P, Nógés T, Ormerod SJ, Panagopoulos Y, Phillips G, Posthuma L, Pouso S, Prudhomme C, Rankinen K, Rasmussen J, Richardo J, Sagouis A, Santos JM, Schäfer RB, Schindegger R, Schmutz S, Schneider SC, Schüßling L, Segurado P, Stefanidis K, Sures B, Thackeray SJ, Turunen J, Uyarra MC, Venohr M, von der Ohe PC, Willby N and Hering D (2020) Impacts of multiple stressors on freshwater biota across spatial scales and ecosytems. Nature Ecology and Evolution 4, 1060–1068.

Blanar CA, Marcogliese DJ and Couillard CM (2011) Natural and anthropogenic factors shape metazoan parasite community structure in mummichog (Fundulus heteroclitus) from two estuaries in New Brunswick, Canada. Folia Parasitologica 58, 240–248.

Branca, Hewitt M, McMaster M, Kirk J, Wang Z, Norwood W and Marcogliese DJ (2016) Parasite community similarity in Athabasca river trout-perch (Perca flavescens) varies with local-scale land use and sediment hydrocarbons, but not distance or linear gradients. Parasitology Research 115, 3853–3866.

Boyce NP and Yamada SB (1977) Effects of a parasite, Eubosentis salvelini (Cestoda: Pseudophyllidea), on the resistance of juvenile sockeye salmon Oncorhyncus nerka to zinc. Journal of the Fisheries Research Board of Canada 406, 704–709.

Braicovich PE, McMaster M, Glozier NE and Marcogliese DJ (2020) Distribution of parasites of slimy sculpin Cottus cognatus Richardsson, 1836 (Scorpaeniformes: Cottidae) in the Athabasca drainage, Alberta, Canada, and their relation to water quality. Parasitology Research 119, 3243–3254.

Brázová T, Hanzelová V and Miklísová D (2012) Bioaccumulation of six PCB indicator congeners in a heavily polluted water reservoir in Eastern Slovakia: tissue-specific distribution in fish and their parasites. Parasitology Research 111, 779–786.

Brázová T, Hanzelová V, Miklísová D, Salamín P and Vidal-Martínez VM (2015) Host-parasite relationships as determinants of heavy metal concentrations in perch (Perca fluviatilis) and its intestinal parasite infection. Ecotoxicology and Environmental Safety 122, 551–556.

Buchmann K and Bresciani J (2006) Monogenea (Pleymyt Platyhelminthes). In Woo PTK (ed.), Fish Diseases and Disorders: Protozoan and Metazoan Infections, vol. 1. Wallingford: CAB International, pp. 297–344.

Carreras-Aubets M, Montero FE, Kostadinova A and Carrasson M (2012) Parasite communities in the red mullet, Mullus barbatus L., respond to small-scale variation in the levels of polychlorinated biphenyls in the Western Mediterranean. Marine Pollution Bulletin 64, 1853–1860.

Chakraborty SB (2021) Non-essential heavy metals as endocrine disruptors: evaluating impact on reproduction in teleosts. Proceedings of the Zoological Society London 74, 417–431.

Combes C (1995) Interactions Durables. Ecologie et Évolution du Parasitisme. Paris: Masson.

Dezfui BS, Maestri C, Lorenzoni M, Carosi A, Maynard BJ and Bosi G (2021) The impact of Anguillicoloides crassus (Nematoda) on European eel swinbladder: histopathology and relationship between neuroendocrine and immune cells. Parasitology 148, 612–622.

Díaz-Morales DM, Bommartito C, Vajedamie J, Grabner DS, Rilov G, Wahl M and Sures B (2022) Heat sensitivity of first host and cercariae may restrict parasite transmission in a warming sea. Scientific Reports 12, 1174.

Dzika E, Kusztala A and Kusztala M (2007) Parasites of carp bream, Abramis brama, from lake Jamno, Poland. Helminthologia 44, 222–225.

Eira C, Torres J, Miquel J, Vaqueiro J, Soares AMVM and Vingada J (2009) Trace element concentrations in Proteocephalus macrocephalus (Cestoda) and Anguillicola crassa (Nematoda) in comparison to their fish host, Anguilla anguilla in Rio de Aaveiro, Portugal. Science of the Total Environment 407, 991–998.

Erasmus JH, Zimmermann S, Smit NJ, Malherbe W, Nachev M, Sures B and Wepener V (2022) Human health risks associated with consumption of fish contaminated with trace elements from intensive mining activities in a peri-urban region. Science of the Total Environment 825, 154011.

Fanton H, Franquet E, Logez M and Kaldonski N (2020) Pomphorhynchus laevis manipulates Gammarus pulex behavior despite salt pollution. Freshwater Biology 65, 1718–1725.
Filipovic Marijiv, V, Vrdić Smržić I and Raspob B (2013) Effect of acanthocephalan infection on metal, total protein and metallothionein concentra-
tions in European chub from a Sava river section with low metal contamination. Science of the Total Environment 463–464, 772–780.

Filipovic Marijiv, V, Vrdić Smržić I and Raspob B (2014) Does fish repro-
duction and metabolic activity influence metal levels in fish intestinal para-
sites, acanthocephalans, during fish spawning and post-spawning period?
Chemosphere 112, 449–455.

Frank SN, Goderhardt S, Nachev M, Trubriho A, Klosa W and Sures B (2013) Influence of the cestode Ligula intestinalis and the acanthocephalan Polymorphus minutus on levels of heat shock proteins (HSP70) and metal-
lothioneins in their fish and crustacean intermediate hosts. Environmental Pollution 180, 173–179.

Gabagambi NP, Salvanes A-GV, Midtøy F and Skorping A (2019) The tape-
worm Ligula intestinalis alters the behavior of the fish intermediate host Engraulicypris sardella, but only after it has become infective to the final host. Behavioural Processes 158, 47–52.

Gabrashanska M and Nedeva I (1996) Content of heavy metals in the system fish-cestodes. Parasitologija 38, 58.

Gérard C, Hervé M, Révillac E and Acou A (2016) Spatial distribution and impact of the gill-parasitic Moxazoa alaeae (Monogenea Polypodiphycoteo) on Alosa alosa and A. falkii (Actinopterygii, Clupeidae). Hydrobiologia 763, 371–379.

Gheorghiu C, Cable J, Marcogliese DJ and Scott ME (2007) Effects of waterborne zinc on reproduction, survival and morphometrics of Gyrodactylus turnbulli (Monogenea) on guppies (Poeclia reticulata). International Journal for Parasitology 37, 375–381.

Gheorghiu C, Marcogliese DJ and Scott M (2006) Concentration-dependent effects of waterborne zinc on population dynamics of Gyrodactylus turnbulli (Monogenea) on isolated guppies (Poeclia reticulata). Parasitology 132, 225–232.

Gilbert BM and Avenant-Oldewage A (2017) Trace element and metal seques-
tration in vitellaria and eggs, and reactive oxygen intermediates in a fresh-
water monogenean, Paradiplozoon ichthyoxanthon. PLoS ONE 12, e0177558.

Gilbert BM and Avenant-Oldewage A (2021) Monogeneans as bioindicators: a meta-analysis of effect size of contaminant exposure toward Monogenea (Platyhelminthes). Ecological Indicators 130, 108062.

Giles N (1983) Behavioural effects of the parasite Schistosoma solidus (Cestoda) on an intermediate host, the three-spined stickleback, Gasterosteus aculeatus L. Animal Behaviour 31, 1192–1194.

Goedknap MA, Feis ME, Wegner KM, Luttikhuizen PG, Buschbaum C, Camphuyzen KCI, van der Meer J and Thijtges DW (2016) Parasites and marine invasions: ecological and evolutionary perspectives. Journal of Sea Research 113, 11–27.

Gütinger H and Stumm W (1992) Ecotoxicology: an analysis of the Rhine pollution caused by the Sandoz chemical accident, 1986. Interdisciplinary Science Reviews 17, 127–136.

Heincke RD, Martinussen T and Buchmann K (2007) Microhabitat selec-
tion of Gyrodactylus salaris Malmberg on different salmonids. Journal of Fish Diseases 30, 733–743.

Heinonen J, Kukkonen JVK and Holopainen JI (2001) Temperature- and parasite-induced changes in toxicity and lethal body burdens of penta-
chlorophenol in the freshwater clam Pisidium amnicum. Environmental Toxicology and Chemistry 20, 2778–2784.

Hoole D (1997) The effects of pollutants on the immune response of fish: implications for helminth parasites. Parasitology 99, 219–225.

Hua J, Buss N, Kim J, Orlofske SA and Hoverman JT (2016) Population-
specific toxicity of six insects to the trematode Echinoparyphium. Parasitology 143, 542–550.

Hursky O and Pietrock M (1983) Behavioural effects of the parasite Engraulicypris sardella, but only after it has become infective to the final host. Behavioural Processes 158, 47–52.

Koprivnikar J, Baker RL and Forbes MR (2006) Environmental factors influencing trematode prevalence in grey tree frog (Hyla versicolor) tadpoles in southern Ontario. Journal of Parasitology 92, 997–1001.

Koprivnikar J, Forbes MR and Baker RL (2007) Contaminant effects on host-parasite interactions: atrazine, frogs, and trematodes. Environmental Toxicology and Chemistry 26, 2166–2170.

Krause RJ, McLaughlin DJ and Marcogliese DJ (2010) Parasite fauna of Etheostoma nigrum (Percaieae Etheostomatinae) in localities of varying pollution stress in the St. Lawrence River, Quebec, Canada. Parasitology Research 107, 283–294.

Kuris AM, Heching RE, Shaw JC, Whitney KL, Aguirre-Macedo L, Boch CA, Dobson AP, Dunham EJ, Fredensborg BL, Huspeni TC, Torchin ME and Lafferty KD (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454, 515–518.

Leite LAR, dos Reis Peidra Filho W, de Azevedo RK and Abdallah VD (2021) Proteocephalus macrophthalmus (Cestoda: Proteocephalidae) infecting Chilka kelberi (Chiliformes: Chilidae) as a bioindicator for trace metal accumulation in a neotropical river from Southeastern Brazil. Water, Air, and Soil Pollution 232, 486.

Link M, Schreiner VC, Graf N, Söös E, Bundschuh M, Bates KP, Cimpian M, Sures B, Grabner D, Buse J, Buse J and Schäfer RB (2022) Pesticide effects on macroinvertebrates and leaf litter decomposition in areas with traditional agriculture. Science of the Total Environment 828, 154549.

Marcogliese DJ (2004) Parasites: small players with crucial roles in the eco-
logical theater. EcoHealth 1, 151–164.

Marcogliese DJ (2005) Parasites of the superorganism: are they indicators of ecosystem health? International Journal for Parasitology 35, 705–716.

Marcogliese DJ and Pietrock M (2011) Combined effects of parasites and contaminants on animal health: parasites do matter. Trends in Parasitology 27, 123–130.

Marcogliese DJ, Ball M and Lankester MW (2001) Potential impacts of clear-
cutting on parasites of minnows in small boreal lakes. Folia Parasitologica 48, 269–274.

Marcogliese DJ, Dautremepuis C, Gendron AD and Fournier M (2010) Interactions between parasites and pollutants in yellow perch (Perca flavescens) in the St. Lawrence River, Canada: implications for resistance and tolerance to parasites. Canadian Journal of Zoology 88, 247–258.

Marcogliese DJ, Locke SA, Gélinas M and Gendron AD (2016) Variation in parasite communities in Spottail shiners (Notropis hudonius) linked with precipitation. Journal of Parasitology 102, 27–36.

Morley NJ, Irwin SWB and Lewis JW (2003) Pollution toxicity to the trans-
mission of larval digeneans through their molluscan hosts. Environmental Science and Technology 34, 5540–5549.

Morley NJ, Agostini S, Alliot F, Angelier F, Biard C, Decencière B, Leroux-Coyau M, Milloï A, Ribout C and Goutte A (2021) Parasitism reduces oxidative stress of fish host experimentally exposed to PAHs. Ecotoxicology and Environmental Safety 219, 112322.

Morley NJ, Lewis JW and Hoole D (2006) Pesticide-induced effects on immuno-
logical and physiological interactions in aquatic host-trematode systems: impli-
cations for parasite transmission. Journal of Helminthology 80, 137–149.

Münderle M, Sures B and Taraschewski H (2004) Influence of Aegrellucilla crassus (Nematoda) and Ichthyophthirius multifiliis (Ciliophora) on swimming activity of European eel Anguilla anguilla. Diseases of Aquatic Organisms 60, 133–139.

Museth J (2001) Effects of Ligula intestinalis on habitat use, predation risk and catchability in European minnows. Journal of Fish Biology 59, 1070–1080.

Nachev M and Sures B (2009) The endohelminth fauna of barbel (Barbus barbus) correlates with water quality of the Danube River in Bulgaria. Parasitology 136, 545–552.

Nachev M, Rozdina D, Michler-Kozma DN, Raikova G and Sures B (2022) Metal accumulation in eco- and endoparasites from the anadromous fish, the Pontic shad (Alosa alosa). Parasitology 149, 496–502.

Ösoy-Okoth E, Wim A, Osano O, Kraak MH, Ngure V, Makwaji J and Orina PS (2010) Use of the fish endoparasite Ligula intestinalis (L. 1758) in an intermediate cyprinid host (Rasbropoebula argentea) for biomoo-
nitoring heavy metal contamination in Lake Victoria, Kenya. Lakes and Reservoirs: Research and Management 15, 63–73.

Paller VGV, Resurreccion DJB, de la Cruz CPP and Bandal MZ (2016) Acanthocephalan parasites (Acanthocephala sp.) of Nile Tilapia (Oreochromis niloticus) as Biosink of lead (Pb) contamination in a Philippine freshwater lake. Bulletin of Environmental Contamination and Toxicology 96, 810–815.
Shafaquat AS, Syed T, Showket AG, Shazia A, Uzma N and Iram A (2015) 
Acanthocephalan infestation in fishes – a review. Journal of Zoology Studies 
2, 33–38.

Sokolowski MS and Dove ADM (2006) Histopathological examination of wild 
American eels infected with Anguillicola crassus. Journal of Aquatic Animal 
Health 18, 257–262.

Soldánová M, Selbach C and Sures B (2016) The early worm catches the bird? 
Productivity and patterns of Trichobilharzia szidati cercarial emission from 
Lymnaea stagnalis. PLoS ONE 11, e0149678.

Sures B (2008a) Environmental parasitology. Interactions between parasites 
and pollutants in the aquatic environment. Parasite 15, 434–438.

Sures B (2008b) Host-parasite interactions in polluted environments. Journal 
of Fish Biology 73, 2133–2142.

Sures B and Knopf K (2004) Individual and combined effects of cadmium 
and 3,3′,4,4′-pentachlorobiphenyl (PCB 126) on the humoral immune 
response in European eel (Anguilla anguilla) experimentally infected with 
larvae of Anguillicola crassus (Nematoda). Parasitology 128, 445–454.

Sures B, Siddall R and Taraschewski H (1999) Parasites as accumulation 
indicators of heavy metal pollution. Parasitology Today 15, 16–21.

Sures B, Knopf K and Kloos W (2001) Induction of stress by the swimbladder 
nematode Anguillicola crassus in European eels, Anguilla anguilla, after 
repeated experimental infection. Parasitology 123, 179–184.

Sures B, Desfuli BS and Krug HF (2003) The intestinal parasite 
Pomphorhynchus laevis (Acanthocephala) interferes with the uptake and 
accumulation of lead (210Pb) in its fish host chub (Leuciscus cephalus). 
International Journal for Parasitology 33, 1617–1622.

Sures B, Lutz I and Kloos W (2006) Effects of infection with Anguillicola crus-
sus and simultaneous exposure with Cd and 3,3′,4,4′-pentachlorobiphenyl 
(PCB 126) on the levels of cortisol and glucose in European eel (Anguilla 
anguilla). Parasitology 132, 281–288.

Sures B, Nachev M, Selbach C and Marcogliese DJ (2017) Parasite responses 
to pollution: what we know and where we go in ‘Environmental parasit-
ology’. Pathozoites and Vectors 10, 1–19.

Svensson PA, Eghbal R, Eriksson R and Nilsson E (2022) How cunning is 
the puppet-master? Cestode-infected fish appear generally fearless. 
Parasitology Research 121, 1305–1315.

Taglioretti V, Rossin MA and Timi JT (2018) Fish-trematode systems as 
indicators of anthropogenic disturbance: effects of urbanization on a 
small stream. Ecological Indicators 93, 759–770.

Taslima K, Al-Emran M, Rahman MS, Hasan J, Ferdous Z, Rohani MF and 
Rohani M (2021) Associations between pharmaceutical 
substances and inhibition of growth and development of 
Notropis hudsonius (Cyprinidae). Toxins 13, 759–770.

Tien Tran, Trinh TD and Maskell H (2018) The role of biotic factors in 
the transmission of free-living endohelminth stages. Parasitology 
135, 407–426.

Thilagaratne IDSIP, McLaughlin JD and Marcogliese DJ (2007) Effects 
of pollution and parasites on biomarkers of fish health in spottail shiners 
Notropis hudsonius (Clinion). Journal of Fish Biology 71, 519–538.

Tierney KB, Farrell AP and Brauner CJ (eds) (2013) Fish Physiology: Organic 
Chemical Toxicology of Fishes. London: Elsevier.

Torres J, Eira C, Miquel J, Ferrer-Maza D, Delgado E and Casadevall M 
(2015) Effect of intestinal tapeworm Clastobothrium crassicercis on concen-
trations of toxic elements and selenium in European Hake Merluccius merluccius from the Gulf of Lion (Northwestern Mediterranean Sea). 
Journal of Agricultural and Food Chemistry 63, 9549–9556.

Trubiroha A, Kroupova H, Wuertz S, Frank SN, Sures B and Kloas W 
(2010) Naturally-induced endocrine disruption by the parasite Ligula intes-
nalis (Cestoda) in roach (Rutilus rutilus). General and Comparative 
Endocrinology 166, 234–240.

Trubiroha A, Kroupova H, Frank SN, Sures B and Kloos W (2011) Inhibition 
of gametogenesis by the cestode Ligula intestinalis in roach (Rutilus rutilus) 
is attenuated under laboratory conditions. Parasitology 138, 648–659.

Turcekova L and Hanzelova V (1999) Concentrations of Cd, As and Pb in 
non-infected and infected Perca fluviatilis with Proteocephalus parcerae. 
Helminthologia 36, 31–39.

Van Urk G, Kerkum F and Van Leeuwen CJ (1993) Insects and insecticides 
in the lower Rhine. Water Research 27, 205–213.

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