



Contents lists available at ScienceDirect

Chemosphere

journal homepage: www.elsevier.com/locate/chemosphere

Review

Accumulation of persistent organic pollutants in parasites

T.T. Yen Le^{a,*}, Laurie Rijdsdijk^a, Bern Sures^b, A. Jan Hendriks^a^a Department of Environmental Science, Institute for Water and Wetland Research, Radboud University Nijmegen, The Netherlands^b Department of Aquatic Ecology and Centre for Water and Environmental Research (ZWU), University of Duisburg Essen, Germany

HIGHLIGHTS

- Effects of parasite infections on the accumulation of pollutants reviewed.
- Fractionation of POPs between parasites and their hosts discussed.
- Relationships between accumulation of POPs and chemical properties examined.
- Accumulation of POPs in host–parasite systems and lipid content investigated.
- Effects of physiological and behavioural processes of parasites described.

ARTICLE INFO

Article history:

Received 10 September 2013

Received in revised form 17 January 2014

Accepted 25 January 2014

Available online xxxx

Keywords:

Parasite

Organic compounds

Accumulation

Hydrophobicity

Lipid content

Trophic level

ABSTRACT

Organisms are simultaneously exposed to various stressors, including parasites and pollutants, that may interact with each other. Research on the accumulation of organic compounds in host–parasite systems is scant compared to studies on parasite–metal interactions and mainly focuses on intestinal endoparasites. We reviewed factors that determine the accumulation of persistent organic pollutants (POPs) in host–parasite systems. The wet/dry weight-based concentration of POPs in these parasites is usually lower than that in host tissues because of lower lipid contents in the parasites. However, the fractionation of the pollutants into parasites and their hosts may vary, depending on developmental stages in the life cycle of the parasites. Developmental stages determine the trophic relationship and the taxon of the parasite in the host–parasite systems because of different feeding strategies between the stages. Lipid-corrected concentrations of organic chemicals in the host are usually higher than those in the endoparasites studied. This phenomenon is attributed to a number of physiological and behavioural processes, such as feeding selectivity and strategy and excretion. Moreover, no significant relationship was found between the accumulation factor (i.e. the ratio between the lipid-corrected concentrations in parasites and in their hosts) for polychlorinated biphenyls and either hydrophobicity or molecular size. At the intermediate hydrophobicity, larger and more lipophilic compounds are accumulated at higher levels in both parasites and the host than smaller and less lipophilic compounds. The bioaccumulation of POPs in parasites is affected by some other abiotic, e.g. temperature, and biotic factors, e.g. the number of host species infected by parasites.

© 2014 Elsevier Ltd. All rights reserved.

Contents

1. Parasitism and chemical exposure	00
2. Bioaccumulation of persistent organic pollutants in host–parasite systems	00
2.1. Effects of parasites on the accumulation in the host	00
2.2. Fractionation of pollutants in host–parasite systems	00
3. Factors affecting the accumulation of persistent organic pollutants in parasites	00
3.1. Chemical properties of pollutants	00
3.2. Biological traits	00

* Corresponding author. Address: Department of Environmental Science, Faculty of Science, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands. Tel.: +31 (0)24 365 23 93; fax: +31 (0)24 355 34 50.

E-mail addresses: YenLe@science.ru.nl, yenle1012@gmail.com (T.T. Yen Le).

<http://dx.doi.org/10.1016/j.chemosphere.2014.01.036>

0045-6535/© 2014 Elsevier Ltd. All rights reserved.

3.3. Physiological and behavioural processes of parasites	00
3.4. Other biotic and abiotic factors	00
4. Conclusion	00
References	00

1. Parasitism and chemical exposure

The interaction between parasitism and pollution is complex. Both parasites and pollutants have been reported to negatively affect the host's health. However, combined effects of parasite infection and chemical exposure on the host are still largely unknown, in particular for persistent organic pollutants (POPs) (Sures, 2008; Marcogliese and Pietrock, 2011). These chemicals are highly toxic and stable in the environment. Slow metabolism of these substances accounts for their biomagnification through food chains as reported in literature (Rasmussen et al., 1990; Kidd et al., 1998; Jones and de Voogt, 1999; Fisk et al., 2001). The bioaccumulation level of POPs varies, depending on their octanol–water partition coefficients, i.e. K_{OW} (Govers et al., 1996; Fisk et al., 2001). For example, compounds with $\log K_{OW}$ of 4–5 or higher may be partitioned into the organic matter phase and therefore be accumulated in large amounts through food chains (Thomann and Connolly, 1984).

Parasite infection is another potential stressor to organisms. Parasites may disrupt a number of physiological processes in their host (Frank et al., 2013). For example, parasites increased the glycogen contents in crustacean *Gammarus pulex* and brine shrimps *Artemia* spp. (Amat et al., 1991; Plaistow et al., 2001). Various effects of a simultaneous presence of parasites and pollutants on the host have been reported (Sanchez-Ramirez et al., 2007; Marcogliese and Pietrock, 2011). Although direct significant relationships between parasite intensities and the level of exposure to organic substances are often not obvious, increased POP concentrations may lead to damage to the immune system of the host, thereby increasing parasite densities (Sagerup et al., 2009). For instance, exposure to pollutants such as polychlorinated biphenyls (PCB) inhibited the production of antibodies to *Anguillicola crassus* and *Vibrio anguillarum* in European eel *Anguilla anguilla* and catfish *Ictalurus punctatus*, respectively (Regala et al., 2001; Sures and Knopf, 2004), thus increasing infection in the hosts (Sures, 2006). The decrease in the antibodies to *A. crassus*, which resulted from a combination of chemical exposure and parasitism, additionally increased the concentration of serum cortisol in eels (Sures, 2006). Another combined effect of parasitism and chemical exposure is the uptake and use of the substances that are essential for the growth, maintenance, and development of the host, such as sterols (Sures, 2006).

Studies on the accumulation of organic pollutants in parasites are scarce in comparison to those for metals because of the suggestion on the fractionation of organic compounds between parasites and their hosts. The suggestion is related to the commonly-observed bioaccumulation pattern of organic chemicals, i.e. lipophilic substances are stored in lipids (Sures, 2004). With lower lipid contents in most parasite taxa compared to those in the host, the accumulation level of lipophilic substances on the basis of dry or wet weight (termed as weight-based concentrations in the following sections) is expected to be lower in parasites than in the host tissues (Heinonen et al., 1999, 2000). Moreover, investigations for organic compounds primarily focus on the effect of parasitism on the accumulation in the host while ignoring other interactions between parasites and the pollutants. An understanding of the accumulation of organic substances in parasites provides better insight into the interactions between parasites and these pollutants

and effects of their co-existence on the host as well. Linking the bioaccumulation to chemical properties such as hydrophobicity (represented by the octanol–water partition coefficient K_{OW}) and species traits enables estimations of pollutant concentrations in organisms. Furthermore, this relationship might be integrated into models that have been developed for estimating bioaccumulation of organic compounds in the host to obtain a mechanistic understanding of the fractionation of these pollutants in host–parasite systems. The present study aimed to review the factors, including chemical properties and biological traits, that play an important role in determining the accumulation of POPs in parasites in order to facilitate the development of a mechanistic model simulating chemical accumulation in host–parasite systems.

2. Bioaccumulation of persistent organic pollutants in host–parasite systems

2.1. Effects of parasites on the accumulation in the host

Parasites have been reported to have different effects on the bioaccumulation of various pollutants, including POPs, in the host. Heinonen et al. (2000) found that uninfected clams *Pisidium amnicum* accumulated benzo(a)pyrene (BaP) and 2,4,5-trichlorophenol (TCP) at significantly higher levels than clams infected with trematodes on the basis of dry weight. By contrast, concentrations of organic halogen compounds in infected freshwater molluscs were higher than those in uninfected controls because of the increase in the carbohydrate metabolism rates induced by the digeneans (Morley et al., 2006). The impacts of parasites on the bioaccumulation in the host may be related to physiological effects on the host (Sures, 2006; Marcogliese and Pietrock, 2011). Changes in the bioaccumulation of POPs in the host, in turn, affect the tolerance of the host to the contaminants. For instance, Heinonen et al. (2000) found increased survival and lethal body burdens of infected clams compared to those of uninfected individuals following exposure to pentachlorophenol (PCP). It was suggested that the increased tolerance is associated with the changing internal distribution of PCP in the host, which was caused by the PCP accumulation in the lipid-rich parasites (Morley et al., 2006).

2.2. Fractionation of pollutants in host–parasite systems

In general, parasites can be classified into ecto- and endoparasites with different patterns of chemical fractionation between these parasites and their hosts. Chemical fractionation between ectoparasites and their hosts depends on feeding strategies of the parasites as these parasites cannot take up amino acids via their keratinised cuticle (Iken et al., 2001; Pinnegar et al., 2001; Deudero et al., 2002). Most ectoparasites feed on the lipid-rich blood of the host (Romestand and Trilles, 1976). Concentrations of organic substances in the ectoparasites are therefore expected to be higher than those in their hosts, similar to the enrichment of ^{15}N in ectoparasites observed by Deudero et al. (2002). In addition, some ectoparasites take up nutrients by inserting their siphon into the gut and therefore assimilate the same food material as their hosts (Iken et al., 2001). Similarly, chemical fractionation into endoparasites and their hosts varies, depending on a number of factors such as trophic relationships, location in the host, and food selectivity as

described in more detail in the following section. Most of the endoparasites cannot synthesise long-chain fatty acids and therefore take up lipids directly from their hosts (Köhler and Voigt, 1988). Endoparasites living in the host's intestine have the same food as the host while endoparasites feeding on the host's tissues or fluids can be considered as in one trophic level higher than their hosts (Iken et al., 2001). Until now, the accumulation of POPs has been primarily studied in intestinal endoparasites.

As mentioned in the first section, on the basis of dry or wet weight, concentrations of POPs are usually lower in parasites than in their hosts (Sures, 2004). For example, concentrations of POPs in the larval trematode *Bunodera luciopercae* and the adult cestode *Eubothrium crassum* were lower than those in their hosts, i.e. freshwater clam *P. amnicum* and salmon *Salmo salar*, respectively (Heinonen et al., 1999; Persson et al., 2007). Despite this general trend, the chemical fractionation in host–parasite systems is ambiguous, depending on a variety of physiological and behavioural processes of the parasites as discussed in more detail in next section (Boag et al., 1998; Pinnegar et al., 2001). This ambiguity has been demonstrated by the opposite of the above fractionation pattern as reported by Heinonen et al. (1999) at the redia stage of *Palaeorchis crassus*, for example. This difference is mainly related to the life cycle and physiological features of *P. crassus*, which produces cercariae through rediae (Rantanen et al., 1998). Rediae

already have a mouth and intestine and are therefore able to feed on the host tissues, i.e. the gonads. Accordingly, they may accumulate chemicals from the clam tissue while feeding on host organs. Parasite stages (digenean rediae, some nematode larvae) or taxa (e.g. different nematode species) that prey upon the host tissues can be considered as in a higher trophic level than their host (own unpublished data). There is no general classification for the trophic level of parasites as their trophic position depends on their taxonomic group as well as on their developmental stage. For example, specific larval stages of digenean trematodes (rediae) or nematodes (fourth stage larvae) directly feed on host tissues and can therefore reach a higher trophic level than their intermediate hosts (Persson et al., 2007; own unpublished data). By contrast, adult cestodes (Persson et al., 2007) or acanthocephalans (own unpublished data) partly use the same diet as their hosts supplemented by some molecules, e.g. fatty acids, of host origin (Aitzetmüller et al., 1994). In addition, excretion by parasites and their hosts may be different, leading to different accumulation levels as demonstrated by higher concentrations of lindane in metacercariae of *Bucephaloides gracilescens* than in the host tissue (Ruus et al., 2001).

Lipid-corrected concentrations in the parasites investigated in previous studies (primarily intestinal endoparasites as mentioned above) were usually lower than the corresponding concentrations

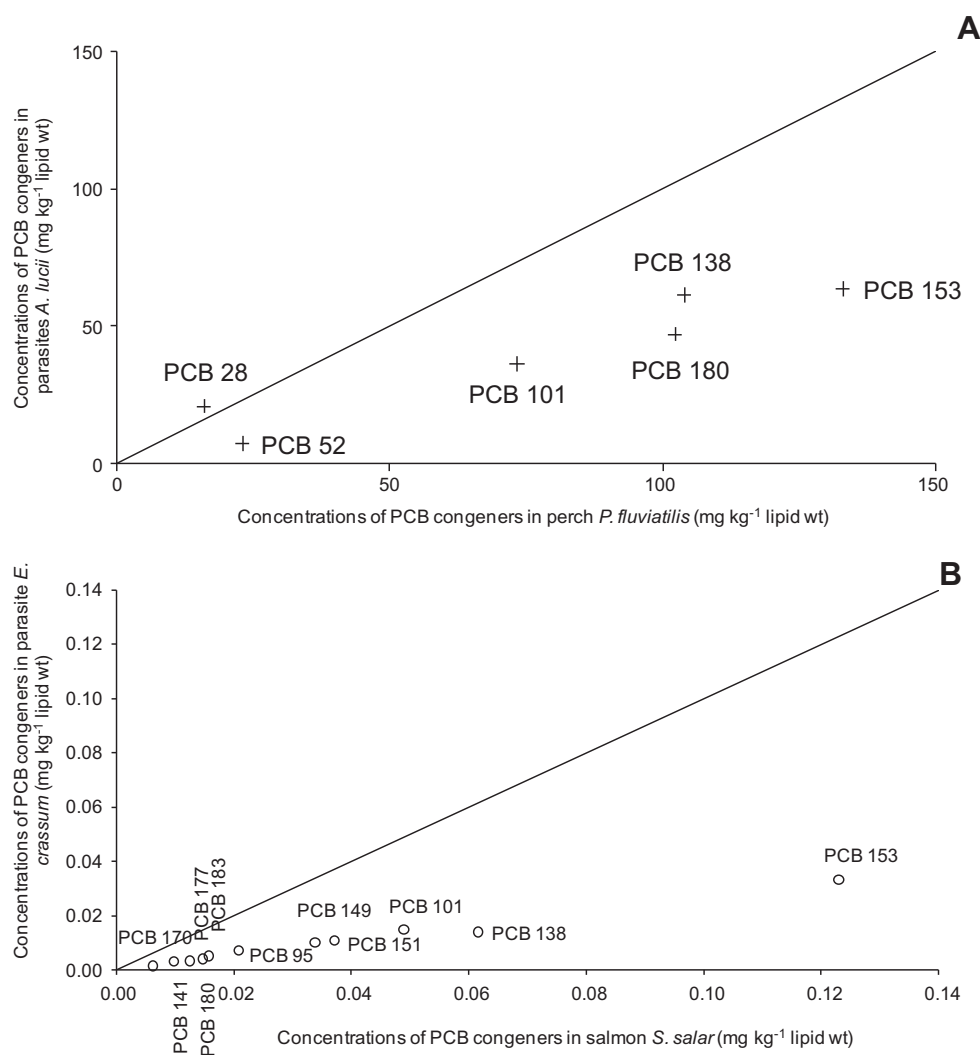


Fig. 1. Comparison of the lipid-based concentrations of PCB congeners in parasites *Acanthocephalus luci* (A) and *Eubothrium crassum* (B) and their hosts *Perca fluviatilis* and *Salmo salar* measured by Brázová et al. (2012) and Persson et al. (2007), respectively. The solid line represents a 1:1 relationship.

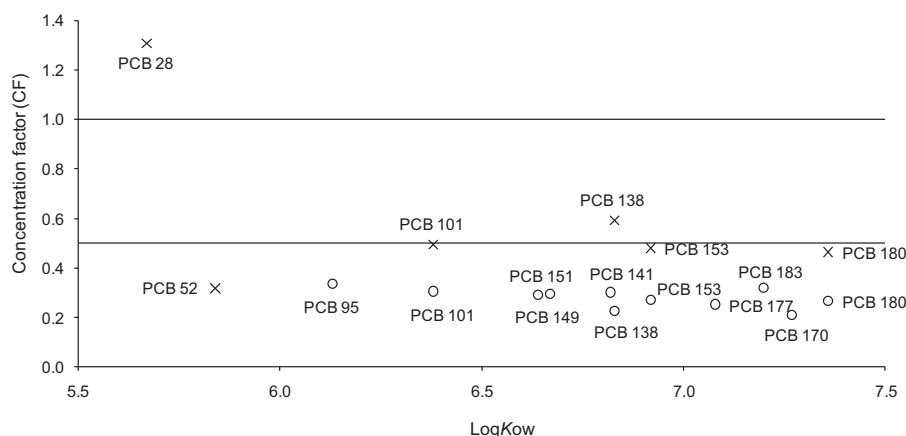


Fig. 2. Variability in the concentration factor, i.e. the ratio between the lipid-corrected concentration in parasites and in the host, for PCB congeners with the $\log K_{OW}$ (Hawker and Connell, 1988) of these substances based on the data generated by Brázová et al. (2012) (represented by multiplication points) and by Persson et al. (2007) (represented by circles).

in their hosts. For instance, lipid-based concentrations of PCB congeners except PCB 28 were lower in the intestinal parasite *Acanthocephalus lucii* than in various tissues of the host fish *Perca fluviatilis* (Brázová et al., 2012; Fig. 1A). The difference in the accumulation level between the parasite and the host varied between congeners, depending on their hydrophobicity and molecular size. In general, the deviation between the concentrations in the parasite *A. lucii* and in the fish *P. fluviatilis* increased with increasing $\log K_{OW}$ and molecular size (Fig. 1A). Parasites, which do not have a gastrointestinal tract (GIT) such as acanthocephalans and cestodes, have a lower synthetic capacity to take up chemicals from the host tissue via passive transport (Jobling, 1995; Cox, 2001). Consequently, it is more difficult for these parasites to take in larger molecules from their hosts (Persson et al., 2007), accounting for the increasing difference in the lipid-corrected concentration between the fish and the acanthocephalan with the increasing molecular size as shown in Fig. 1A. This explanation, however, does not account for the accumulation of PCB congeners in the cestode *E. crassum* parasitizing in salmon *S. salar* although similar to the above host–parasite system, higher lipid-based concentrations of all the PCB congeners were measured in the host salmon *S. salar* than in *E. crassum* (Fig. 1B). The relationship between chemical properties of pollutants and their bioaccumulation in parasites is discussed in more detail in the following section.

3. Factors affecting the accumulation of persistent organic pollutants in parasites

The level of chemical fractionation in host–parasite systems can be expressed by the concentration factor CF reflecting the ratio between the lipid-corrected concentrations in the parasite and in the host (Sures et al., 1999). Although the trophic relationship is known to be important for chemical accumulation in host–parasite systems as described in the previous section, a common understanding of the relation between developmental stages of a certain parasite taxa and trophic levels is currently missing. The trophic relationship between parasites and their hosts is largely unknown (Williams and Jones, 1994; Boag et al., 1998). Although the use of stable isotope (^{15}N and ^{13}C) analyses will probably help to shed light on these aspects, available data are currently limited (Iken et al., 2001; Pinnegar et al., 2001; Power and Klein, 2004; Persson et al., 2007). Moreover, previous studies (e.g. Iken et al., 2001; Pinnegar et al., 2001) indicate that the trophic level of parasites in food webs cannot be completely revealed by using these stable

isotopes. Alternatively, bioaccumulation in parasites can be linked to other biotic, e.g. lipid content, and abiotic factors, e.g. hydrophobicity and molecular size, in order to facilitate estimating the accumulation by the parasites.

3.1. Chemical properties of pollutants

As described in the first section, bioaccumulation and biomagnification of POPs via food chains have been widely related to their hydrophobicity. However, the variability in the accumulation in parasites between POPs could not be explained by either their hydrophobicity or molecular size (Fig. 2). No significant relationship was found between CF of PCB congeners in *A. lucii* parasitizing in perch *P. fluviatilis* and $\log K_{OW}$ (Brázová et al., 2012; $p > 0.05$; Fig. 2). Similarly, the CF representing the accumulation of PCBs in *E. crassum* parasitizing salmon was not significantly related to their hydrophobicity (Persson et al., 2007; Fig. 2). The lack of significant relationships between CF (Fig. 2) or the biomagnification factor (Persson et al., 2007) of parasites and hydrophobicity may just result from the narrow range of $\log K_{OW}$ studied, i.e. 5.6–7.4 in Brázová et al. (2012) and 6.1–7.4 in Persson et al. (2007). Moreover, the insignificant correlation between CF and hydrophobicity or molecular size of PCBs was attributed to similar accumulation patterns in these parasites and their hosts, i.e. similar contribution of individual congeners to the total accumulation of all congeners. In the intermediate range of hydrophobicity and molecular size, larger and more lipophilic PCB congeners were accumulated at higher levels than smaller and less lipophilic congeners in both the parasites and their hosts (Fig. 1A; Persson et al., 2007; Brázová et al., 2012). However, this general trend did not hold for the smallest or largest molecules (Fig. 2). Furthermore, the same accumulation pattern in the parasites and in the hosts as observed above for PCB congeners may be related to the uptake mechanism of *A. lucii* and *E. crassum*, i.e. feeding on the intestinal content. In other words, for PCB congeners in the intermediate range of hydrophobicity and molecular size, the bioaccumulation in parasites may reflect simple partitioning of the pollutants between lipids in the host GIT and lipids in parasites. The absence of this trend observed for the largest molecules is attributable to the size discrimination (Persson et al., 2007). In addition, a higher concentration factor for PCB 28 compared to more hydrophobic congeners (Fig. 2) may reflect the difference in the accumulation of these compounds in the host, i.e. bioconcentration decreases with the decreasing value of $\log K_{OW}$ (Meylan et al., 1999). Substances with a $\log K_{OW}$ value of smaller

than six are dominantly taken up from the dissolved phase. Therefore, their elimination via metabolic transformation and/or gill excretion might be enhanced (Persson et al., 2007). According to Ruus et al. (2001), lindane ($\log K_{OW} < 6$) was eliminated from the host zebrafish *Brachydanio rerio* at higher rates than from its parasites (Ruus et al., 2001). In addition, the uptake of organic substances with a $\log K_{OW} > 6$ in the hosts can be enhanced because of the fugacity gradient induced by food digestion in the GIT (Persson et al., 2007).

3.2. Biological traits

Lipid contents have been shown to explain much of the variation in wet weight concentrations of organic compounds, indicating that POPs have higher tendency to partition in lipids than in the aqueous phase (Jones and de Voogt, 1999; Hendriks et al., 2001; Arnot and Gobas, 2004). As such, lipids are the primary tissue for the accumulation of hydrophobic organic pollutants (Paterson et al., 2007). This is consistent with the lower dry/wet weight-based concentrations of organic substances in parasites compared to the level in their hosts as mentioned above (Heinonen et al., 2000; Persson et al., 2007). However, concentrations of organic substances in parasites cannot be estimated based on the lipid content only as indicated by the deviation of the biomagnification factor (i.e. the ratio between the concentrations in *E. crassum* and in the diet) from 1 (Persson et al., 2007). This is further demonstrated by the observation that, for most of the PCB congeners, lipid-corrected concentrations were higher in the hosts than in parasites ($CF < 1$; Fig. 2). According to Kidd et al. (1995), trophic level, as expressed by the content of ^{15}N , is a better indicator of the accumulation of organochlorine compounds than the lipid content. However, this was not observed for the parasite *E. crassum* (Persson et al., 2007). In other words, the organochlorine content in parasites could not be explained by either the lipid content or the trophic level only, contrasting with the findings found for other organisms by Bentzen et al. (1996).

3.3. Physiological and behavioural processes of parasites

As described in previous sections, the lipid-corrected concentrations of organic substances in intestinal endoparasites are expected to be similar to the concentrations in their hosts because they assimilate the same food. In general, the accumulation of chemicals in organisms occurs as a balance of influx and efflux. On the one hand, it has been suggested that the pattern of PCBs accumulation in the endoparasites studied is mainly determined by passive uptake of free fatty acids via diffusion, rather than direct (transport of short-chain fatty acids via ion channels or carrier molecules) or active (absorption of amino-acids and monosaccharides against a concentration gradient) uptake (Köhler and Voigt, 1988; Persson et al., 2007). This is supported by the findings that the accumulation pattern of PCB congeners expressed by relative contribution of individual congeners in the host is similar to that in parasites as presented in previous sections. On the other hand, it has been reported that excretion from the host is substantially faster than from the parasites for substances with $\log K_{OW}$ lower than 6 as discussed previously. More hydrophobic compounds are also more likely to be excreted at higher rates in the host than in parasites because of the GIT, although the difference in the excretion between the host and the parasites for these compounds may be smaller than the discrepancy for compounds with $\log K_{OW} < 6$.

What factors potentially account for higher lipid-corrected concentrations of PCB congeners in the host compared to those in parasites? This phenomenon has been frequently reported in literature as reviewed above and is attributable to specific physio-

logical and behavioural processes of parasites. These processes vary between different parasite groups, such as trematoda, cestoda, acanthocephalan, and nematode, and between different developmental stages. For instance, endoparasites have developed mechanisms for food selectivity, affecting the chemical fractionation between these parasites and their hosts (Hare et al., 1991; Deudero et al., 2002). Many endoparasites, like cestodes and acanthocephalans, take up nutrient molecules from the surrounding medium through their body wall (Heinonen et al., 1999; Randall et al., 2002) as they lack a mouth and intestines. These endoparasites are surrounded by nutrient-rich tissues or alimentary canal fluids of their hosts (Randall et al., 2002). Some larval endoparasites are capable of taking up amino acids directly via body surface, host's blood, or fluids (Wilson and Poe, 1974; Rutherford et al., 1977; Barrett, 1981). Adult acanthocephalans take up nutrients like lipids through different regions of the body wall such as the trunk and preasoma and may be able to re-allocate resources in their own favour to obtain all nutrients (Hammond, 1968; Plaistow et al., 2001). With the heavily keratinised cuticles, adult nematodes, which usually live in the host's gut, cannot differentially select food as the larval nematodes (Pinnegar et al., 2001). In addition, the chemical fractionation between endoparasites and their hosts depends on the location of the intestinal parasites in the gut (Iken et al., 2001). In particular, nematodes that inhabit the host's stomach, before the intestine, may accumulate substances at different levels from that of their hosts. This difference results from different enzyme activities and feeding selectivity of the hosts and the parasites (Iken et al., 2001). This explanation accounts for the weak correlation in the fatty-acid composition of the nematodes and the host tissues (Barrett, 1981). The differences in the fatty acid composition of the parasites and the host intestine were additionally observed by Aitzetmüller et al. (1994). In the hind part of the intestine (behind the stomach), food has been partially processed by the host. Therefore, trematodes inhabiting the hind part of the intestine and the host assimilate the same food material (Iken et al., 2001). As a result, the fatty acid composition of the parasites is well correlated to that in the surroundings (Barrett, 1981). In addition, it is easier for the parasites to utilise the processed food.

The chemical fractionation between parasites and their hosts may differ between developmental stages in the parasites' life cycle as a result of different feeding strategies, growth rates, locations in the hosts' intestine, and trophic levels. For instance, at the stages within the host, i.e. plerocercoid (cestodes) and L3 (nematodes), parasites have the highest growth and nutrient uptake rate (Bush et al., 2001). In addition, juvenile nematodes can absorb food directly through the body surface while adult nematodes take up food via a digestive tract (Arme, 1976). This difference affects their feeding selection as described above. Different feeding strategies have been additionally reported for the copepod *Lernaocera branchialis*, i.e. the copepodid mainly feeds on tissues and mucus of the gill epithelia while the adult parasite utilises the vessel walls (Sproston, 1942; Mann, 1970). The fatty-acid composition of parasites may vary between different developmental stages, too, because of different locations of the parasites in the host's intestine as mentioned above. The dependence of the chemical partitioning in host-parasite systems on the developmental stage in parasites' life cycle is further added by variations in the host species between the developmental stages. For instance, the accumulation in the parasites inhabiting the definitive host may occur as a result of a combination with the infection in the previous host as exemplified by the above case of *P. crassus*, which parasitizes clam first before infesting fish such as perch.

The above discussion about the influence of physiological and behavioural processes of parasites on the chemical fractionation in host-parasite systems is consistent with the findings of Olive et al. (2003). These authors concluded that the direction and

magnitude of the partition between parasites and their hosts occurred as a result of feeding rate, excretion rate, assimilation efficiency, and feeding selectivity of the parasites. Due to the interference of these factors, the relationships between parasites and their hosts differ from the relationships of predators feeding on the prey's bulk tissues (Deudero et al., 2002).

3.4. Other biotic and abiotic factors

Besides chemical properties of pollutants and species features as discussed in Sections 3.1–3.3, the bioaccumulation in host–parasite systems is affected by some other biotic and abiotic factors as listed by Blana et al. (2009). For instance, stronger interactions were found between chemical exposure and infection with monoxenous parasites, i.e. parasitizing only one host, than with heteroxenous parasites, i.e. infecting multi host species. This is because the population of monoxenous parasites is more sensitive to pollutants than the population of heteroxenous parasites (Blana et al., 2009). Heteroxenous parasites are able to take up and accumulate various pollutants at different trophic levels, depending on developmental stages in their life cycles. Temperature is another abiotic factor that influences the bioaccumulation in host–parasite systems as it controls a variety of physiological processes. Concentrations of BaP and TCP in *P. amnicum* infected with *P. crassus* at 4 °C were significantly lower than those at 15 °C, attributed to varying uptake (Heinonen et al., 2000). The uptake of TCP in *P. amnicum* was 10 and 17 times lower at 4 °C than at 15 °C (Heinonen et al., 2000). Consequently, the chemical fractionation between parasites and their host varies, depending on temperature. At 20 °C, the TCP concentration in *P. crassus* was higher than the concentration in their hosts' tissues. At lower temperatures, there was no significant difference between the TCP contents in the parasite and in the host (Heinonen et al., 1999).

4. Conclusion

The co-existence of parasite infection and chemical exposure has various effects on the accumulation of POPs in the host. Parasites are able to accumulate POPs, affecting the partition of these pollutants into the host. Despite lower lipid contents in parasites compared to their hosts, weight-based concentrations of organic compounds have been observed to be higher in parasites than in their hosts for some host–parasite systems. For these cases, chemical accumulation in the parasites may be a better indicator of contamination than the accumulation in their hosts. Moreover, the chemical fractionation between parasites and their hosts varies, depending on the trophic relationships in the host–parasite system (Section 2.2). The chemical accumulation in the parasites assimilating the same food materials as their hosts can be considered as results of passive partitioning between lipids of the parasites and of the host tissue. For such host–parasite systems, no significant difference between pollutant concentrations in the hosts and the parasites would be expected. By contrast, parasites that consume the host's tissue can be considered as in a higher trophic level and therefore probably accumulate substances at a higher level than their hosts. However, deviations from these predictions have been reported, attributed to the interference of physiological and behavioural processes of parasites such as food selectivity. Moreover, the trophic relationship in host–parasite systems depends on the developmental stages in the parasites' life cycle because of the variations in feeding strategies between different stages (Sections 2.2 and 3.3). These factors interfere the chemical fractionation between parasites and their hosts as demonstrated by lower lipid-corrected concentrations of POPs in intestinal parasites than in their hosts, which cannot be explained by lipid

content-based on fugacity. Consequently, bioaccumulation models for organic compounds, which have usually been developed based on the hydrophobicity and molecular size of chemicals and the lipid content of organisms, may not be applicable to parasites. Besides these chemical properties and biological trait, physiological and behavioural processes, which vary between different parasite groups and developmental stages and determine trophic relations in host–parasite systems, should be considered to enable estimating accumulation of organic substances in parasites. These observations emphasize the importance of further studies on the accumulation of organic compounds in host–parasite systems.

References

- Aitzetmüller, K., Taraschewski, H., Filipponi, C., Werner, G., Weber, N., 1994. Lipids of fish parasites and their hosts: fatty acids of phospholipids of *Paratenus ambigua* and its host eel (*Anguilla anguilla*). *Comp. Biochem. Physiol.* 109B, 383–389.
- Amat, F., Gozalbo, J.C., Navro, J.C., Hontoria, F., Varo, I., 1991. Some aspects of *Artemia* biology affected by cestode parasitism. *Hydrobiologia* 212, 39–44.
- Arme, C., 1976. Feeding. In: Kennedy, C.R. (Ed.), *Ecological Aspects of Parasitology*. North Holland Publishing Company, Amsterdam, pp. 75–97.
- Arnot, J.A., Gobas, F.A.P.C., 2004. A food web bioaccumulation model for organic chemicals in aquatic ecosystems. *Environ. Toxicol. Chem.* 23, 2343–2355.
- Barrett, J., 1981. *Biochemistry of Parasitic Helminths*. Macmillan, London.
- Bentzen, E., Lean, D.R.S., Taylor, W.D., Mackay, D., 1996. Role of food web structure and bioaccumulation of organic contaminants by lake trout (*Salvelinus namaycush*). *Can. J. Fish. Aquat. Sci.* 53, 2397–2407.
- Blana, C.A., Munkittrick, K.R., Houlihan, J., MacLachly, D.L., Marcogliese, D.J., 2009. Pollution and parasitism in aquatic animals: a meta-analysis of effect size. *Aquat. Toxicol.* 93, 18–28.
- Boag, B., Neison, R., Robinson, D., Scrimgeour, C.M., Handley, L.L., 1998. Wild rabbit host and some parasites show trophic-level relationship for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$: a first report. *Isot. Environ. Health Stud.* 34, 81–85.
- Brázová, T., Hanzelová, V., Miklišová, 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. *Parasitol. Res.* 111, 779–786.
- Bush, A.O., Fernández, J.C., Esch, G.W., Seed, J.R., 2001. Parasitism: The Diversity and Ecology of Animal Parasites. Cambridge University Press, Cambridge.
- Cox, F.E.G., 2001. *Modern Parasitology*. Blackwell Science, Oxford, UK.
- Deudero, S., Pinnegar, J.K., Polunin, N.V.C., 2002. Insights into fish host–parasite trophic relationships revealed by stable isotope analysis. *Dis. Aquat. Org.* 52, 77–86.
- Fisk, A.T., Hobson, K.A., Norstrom, R.J., 2001. Influence of chemical and biological factors on trophic transfer of persistent organic pollutant in the Northwater Polynya Marine Food Web. *Environ. Sci. Technol.* 35, 732–738.
- Frank, S.N., Godehardt, S., Nachev, M., Trubiroha, A., Kloas, W., Sures, B., 2013. Influence of the cestode *Ligula intestinalis* and the acanthocephalan *Polymorphus minutus* on levels of heat shock protein 70 (HSP70) and metallothionein in their fish and crustacean intermediate hosts. *Environ. Pollut.* 180, 173–179.
- Govers, H.A.J., Loonen, H., Parsons, J.R., 1996. Nonlinear dependence of bioconcentration factors on n-octanol–water partition coefficients of chlorinated dibenzofurans and dibenzo-p-dioxins. *SAR QSAR Environ. Res.* 5, 63–78.
- Hammond, R.A., 1968. Some observations on the role of the body wall of *Acanthocephalus ranae* in lipid uptake. *J. Exp. Biol.* 48, 217–225.
- Hare, P.E., Fogel, M.L., Stafford, T.W., Mitchell, A.D., Hoering, T.C., 1991. The isotopic composition of carbon and nitrogen in individual amino acids isolated from modern and fossil proteins. *J. Archaeol. Sci.* 18, 277–292.
- Hawker, D.W., Connell, D.W., 1988. Octanol–water partition coefficients of polychlorinated biphenyl congeners. *Environ. Sci. Technol.* 22, 282–387.
- Heinonen, J., Kukkonen, J.V.K., Holopainen, I.J., 1999. The effects of parasites and temperature on the accumulation of xenobiotics in a freshwater clam. *Ecol. Appl.* 9, 475–481.
- Heinonen, J., Kukkonen, J.V.K., Holopainen, I.J., 2000. Toxicokinetics of 2,4,5-trichlorophenol and benzo(a)pyrene in the clam *Pisidium amnicum*: effects of seasonal temperatures and trematode parasites. *Arch. Environ. Contam. Toxicol.* 39, 352–359.
- Hendriks, A.J., van der Linde, A., Cornelissen, G., Sijm, D.T.H.M., 2001. The power of size. 1. Rate constants and equilibrium ratios for accumulation of organic substances related to octanol–water partition ratio and species weight. *Environ. Toxicol. Chem.* 20, 1399–1420.
- Iken, K., Brey, T., Wand, U., Voigt, J., Junghans, P., 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Prog. Oceanogr.* 50, 383–504.
- Jobling, M., 1995. *Environmental Biology of Fisheries*. Chapman and Hall, London, UK.
- Jones, K.C., de Voogt, P., 1999. Persistent organic pollutants (POPs): state of the science. *Environ. Pollut.* 100, 209–221.
- Kidd, K., Schindler, D.W., Hesslein, R.H., Muir, D.C.G., 1995. Correlation between stable nitrogen isotopes and concentrations of organochlorines in biota from a freshwater food web. *Sci. Total. Environ.* 160 (161), 281–390.

- Kidd, K.A., Hesslein, R.H., Ross, B.J., Koczenski, K., Stephens, G.R., Muir, D.C.G., 1998. Bioaccumulation of organochlorines through a remote freshwater food web in the Canadian Arctic. *Environ. Pollut.* 102, 91–103.
- Köhler, P., Voigt, W.P., 1988. Nutrition and metabolism. In: Mehlhorn, H. (Ed.), *Parasitology in Focus: Facts and Trends*. Springer-Verlag, Berlin, pp. 412–453.
- Mann, H., 1970. Copepoda and Isopoda as parasites of marine fishes. In: Snieszko, S.F., Editor. *A symposium on Diseases of Fishes and Shellfishes*. American Fisheries Society Special Publication No. 5, Washington, pp. 177–189.
- Marcogliese, D.J., Pietrock, M., 2011. Combined effects of parasites and contaminants on animal health: parasites do matter. *Trends Parasitol.* 27, 123–130.
- Meylan, W.M., Howard, P.H., Boethling, R.S., Aronson, D., Printup, H., Gouche, S., 1999. Improved method for estimating bioconcentration/bioaccumulation factor from octanol/water partition coefficient. *Environ. Toxicol. Chem.* 18, 664–672.
- Morley, N.J., Lewis, J.W., Hoole, D., 2006. Pollutant-induced effects on immunological and physiological interactions in aquatic host-trematode systems: implications for parasite transmission. *J. Helminthol.* 80, 137–149.
- Olive, P.J.W., Pinnegar, J.K., Polunin, N.V.C., Richards, G., Welch, R., 2003. Isotope trophic-step fractionation: a dynamic equilibrium model. *J. Anim. Ecol.* 72, 608–617.
- Paterson, G., Drouillard, K.G., Leadley, L.A., Haffner, G.D., 2007. Long-term polychlorinated biphenyl elimination by three size classes of yellow perch (*Perca flavescens*). *Can. J. Fish. Aquat. Sci.* 64, 1222–1233.
- Persson, M.E., Larsson, P., Stenroth, P., 2007. Biomagnification and polychlorinated biphenyl congener distribution in an aquatic predator–prey, host–parasite system. *Environ. Toxicol. Chem.* 26, 837–843.
- Pinnegar, J.K., Campbell, N., Polunin, N.V.C., 2001. Unusual stable isotope fractionation patterns observed for fish host–parasite trophic relationships. *J. Fish Biol.* 59, 494–503.
- Plaistow, S.J., Troussard, J.-P., Cezilly, F., 2001. The effect of the acanthocephalan parasite *Pomphorhynchus laevis* on the lipid and glycogen content of its intermediate host *Gammarus pulex*. *Int. J. Parasitol.* 31, 346–351.
- Power, M., Klein, G.M., 2004. Fish host–cestode parasite stable isotope enrichment patterns in marine, estuarine and freshwater fishes from northern Canada. *Isot. Environ. Health Stud.* 40, 4.
- Randall, D., Burggren, W., French, K., 2002. Energy acquisition: feeding, digestion and metabolism. In: Randall, D., Burggren, W., French, K. (Eds.), *Eckert Animal Physiology Mechanisms and Adaptations*, fifth ed. Freeman and Company, New York, pp. 631–632.
- Rantanen, J.T., Valtonen, E.T., Holopainen, I.J., 1998. Digenean parasites of the bivalve mollusc *Pisidium amnicum* in a small river in eastern Finland. *Dis. Aquat. Org.* 33, 201–208.
- Rasmussen, J.B., Rowan, D.J., Lean, D.R.S., Carey, J.H., 1990. Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. *Can. J. Fish. Aquat. Sci.* 47, 2030–2032.
- Regala, R.P., Rice, C.D., Schwedler, T.E., Dorociak, I.R., 2001. The effects of tributyltin (TBT) and 3,3',4,4'-pentachlorobiphenyl (PCB-126) mixtures on antibody responses and phagocyte oxidative burst activity in channel catfish, *Ictalurus punctatus*. *Arch. Environ. Contam. Toxicol.* 40, 386–391.
- Romestand, M.B., Trilles, J.P., 1976. Production d'une substance anticoagulante par les glandes exocrine cephalothoraciques des isopods Cymothoidae *Meinertia oestroides* et *Anilocra physodes*. *Cr. Acad. Sci.* 282, 663–665.
- Rutherford, T.A., Webster, J.M., Barlow, J.S., 1977. Physiology of nutrient uptake by the entomophilic nematode *Mermis nigrescens* (Mermithidae). *Can. J. Zool.* 55, 1773–1781.
- Ruus, A., Skaare, J.U., Ingebrigtsen, K., 2001. Accumulation of the lipophilic environmental contaminant lindane in metacercariae of *Bucephaloides gracilescens* (trematoda, bucephalidae) in the central nervous system of bullrout *Myoxocephalus scorpius*. *Dis. Aquat. Org.* 48, 75–77.
- Sagerup, K., Savinov, V., Svinova, T., Kuklin, V., Muir, D.C.G., Gabrielsen, G.W., 2009. Persistent organic pollutants, heavy metals and parasites in the glaucous gull (*Larus hyperboreus*) on Spitsbergen. *Environ. Pollut.* 157, 2282–2290.
- Sanchez-Ramirez, C., Vidal-Martinez, V.M., Aguirre-Macedo, L., Rodriguez-Canul, R.P., Ceja-Moreno, V., Gold-Bouchot, G., Sures, B., 2007. *Cichlidogyrus sclerosus* (Monogenea: Ancyrocephalinae) and its host the Nile Tilapia (*Oreochromis niloticus*) as bioindicators of chemical pollution. *J. Parasitol.* 93, 1097–1106.
- Sproston, N.G., 1942. The developmental stages of *Lernaecera branchialis*. *J. Mar. Biol. Assoc. UK* 25, 441–466.
- Sures, B., 2004. Environmental parasitology: relevancy of parasites in monitoring environmental pollution. *Trends Parasitol.* 20, 170–177.
- Sures, B., 2006. How parasitism and pollution affect the physiological homeostasis of aquatic hosts. *J. Helminthol.* 80, 151–157.
- Sures, B., 2008. Host–parasite interactions in polluted environments. *J. Fish Biol.* 73, 2133–2142.
- Sures, B., Knopf, K., 2004. Individual and combined effects of Cd and 3,3',4,4',5-pentachlorobiphenyl (PCB126) 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., Taraschewski, H., 1999. Parasites as accumulation indicators of heavy metal pollution. *Parasitol. Today* 15, 16–21.
- Thomann, R.V., Connolly, J.P., 1984. Model of PCB in the Lake Michigan lake trout food chain. *Environ. Sci. Technol.* 18, 65–71.
- Williams, H., Jones, A., 1994. *Parasitic Worms of Fish*. Taylor & Francis, London.
- Wilson, R.P., Poe, W.E., 1974. Nitrogen metabolism in channel catfish, *Ictalurus punctatus*. III Relative pool sizes of free amino acids and related compounds in various tissues of the catfish. *Comp. Biochem. Physiol.* 48B, 545–556.