

# Eye fluke-induced cataracts in natural fish populations

## Is there potential for host manipulation?

**Journal Article****Author(s):**

Seppälä, O.; Karvonen, A.; Valtonen, E.T.

**Publication date:**

2011-02

**Permanent link:**

<https://doi.org/10.3929/ethz-b-000028156>

**Rights / license:**

[In Copyright - Non-Commercial Use Permitted](#)

**Originally published in:**

Parasitology 138(2), <https://doi.org/10.1017/S0031182010001228>

# Eye fluke-induced cataracts in natural fish populations: is there potential for host manipulation?

O. SEPPÄLÄ<sup>1\*</sup>, A. KARVONEN<sup>2</sup> and E. T. VALTONEN<sup>3</sup>

<sup>1</sup>EAWAG, Swiss Federal Institute of Aquatic Science and Technology, and ETH-Zürich, Institute of Integrative Biology, Überlandstrasse 133, PO Box 611, CH-8600, Dübendorf, Switzerland

<sup>2</sup>Department of Biological and Environmental Science, Centre of Excellence in Evolutionary Research, PO Box 35, FIN-40014, University of Jyväskylä, Finland

<sup>3</sup>Department of Biological and Environmental Science, PO Box 35, FIN-40014, University of Jyväskylä, Finland

(Received 12 May 2010; revised 19 July 2010; accepted 19 July 2010; first published online 27 August 2010)

## SUMMARY

Manipulation of host phenotype (e.g. behaviour, appearance) is suggested to be a common strategy to enhance transmission in trophically transmitted parasites. However, in many systems, evidence of manipulation comes exclusively from laboratory studies and its occurrence in natural host populations is poorly understood. Here, we examined the potential for host manipulation by *Diplostomum* eye flukes indirectly by quantifying the physiological effects of parasites on fish. Earlier laboratory studies have shown that *Diplostomum* infection predisposes fish to predation by birds (definitive hosts of the parasites) by reducing fish vision through cataract formation. However, occurrence of cataracts and the subsequent potential for host manipulation in natural fish populations has remained poorly explored. We studied the occurrence of eye fluke-induced cataracts from 7 common fish species (*Gymnocephalus cernuus*, *Rutilus rutilus*, *Leuciscus leuciscus*, *Alburnus alburnus*, *Osmerus eperlanus*, *Coregonus lavaretus* and *Gasterosteus aculeatus*) from the Bothnian Bay in the Baltic Sea. We found that the parasite-induced cataracts were common in fish and they also reached high levels which are likely to predispose fish to predation. However, we observed such cataracts only in species with the highest parasite abundances, which suggests that only certain hosts may be strongly affected by the infection.

Key words: *Diplostomum*, parasite–host interactions, parasite transmission, predation, Trematoda.

## INTRODUCTION

Several parasite species that are transmitted trophically from prey to predators alter the phenotype (e.g. behaviour, appearance) of their intermediate hosts (reviewed by Moore, 2002). These changes can be beneficial for parasites if they make infected hosts easier prey for target hosts (next hosts in the life cycle) and this way increase parasite transmission efficiency (Rothschild, 1962; Holmes and Bethel, 1972). Indeed, parasite-induced modifications in host phenotype have been shown to predispose hosts to predation in several parasite–host interactions (e.g. Bethel and Holmes, 1973, 1977; Moore, 1983; Lafferty and Morris, 1996; Mouritsen and Poulin, 2003; Lagrue *et al.* 2007; Seppälä *et al.* 2008a), which is why the ability of parasites to induce such effects is widely considered as adaptive host manipulation. However, in many study systems, host manipulation has been studied only under laboratory conditions (but see e.g. Moore 1983; Mouritsen and Poulin, 2003; Lagrue *et al.* 2007). Although laboratory

studies are important when investigating host manipulation experimentally, they can not address the extent of manipulation in natural host populations where it can be affected, for example, by variation in infection dynamics and use of alternative host species. Therefore, more field studies are needed to estimate how common host manipulation is in natural host populations.

In this study, we examined the effect of parasitic eye flukes of the genus *Diplostomum* (Trematoda) on their natural fish hosts. *Diplostomum* parasites infect a wide variety of freshwater and brackish water fish species (Valtonen and Gibson, 1997), and their metacercarial stages induce cataract formation in the eye lenses of fish, which reduces their vision (Rushton, 1937, 1938; Karvonen *et al.* 2004a). In earlier laboratory studies, *Diplostomum* infection has been shown to alter fish behaviour (Crowden and Broom, 1980; Seppälä *et al.* 2004, 2008b) and appearance (Seppälä *et al.* 2005a) so that their vulnerability to avian predators (definitive hosts of the parasites) increases (Seppälä *et al.* 2004, 2005b). The most likely mechanism leading to these effects is the impaired vision of fish due to parasite-induced cataracts; the susceptibility of fish to predation increases with the coverage of cataracts of the lens area (Seppälä *et al.* 2005b). Furthermore, cataract formation and subsequent increase in predation

\* Corresponding author: EAWAG, Swiss Federal Institute of Aquatic Science and Technology, and ETH-Zürich, Institute of Integrative Biology, Überlandstrasse 133, PO Box 611, CH-8600, Dübendorf, Switzerland. Tel: +41 44 823 5348. Fax: +41 44 823 50 28. E-mail: otto.seppaelae@eawag.ch

vulnerability is most intensive after parasites become infective to birds (Seppälä *et al.* 2005b). Therefore, the ability of these parasites to alter host phenotype through cataract formation is likely to be a parasite adaptation to enhance transmission to bird hosts.

Most of the previous evidence, however, comes from laboratory studies using farmed rainbow trout (*Oncorhynchus mykiss*) as a model host species, which is why the occurrence of manipulation in natural fish populations is poorly understood. Based on the laboratory evidence, however, the degree of manipulation is linked directly to the coverage of parasite-induced cataracts (Seppälä *et al.* 2005b). Thus, potential for manipulation in natural populations could be approached indirectly by using cataract coverage as a proxy for manipulation. In an earlier study, parasite-induced cataracts have been observed in natural populations of walleye (*Stizostedion vitreum*) and white sucker (*Catostomus commersoni*) (Marcogliese *et al.* 2001) suggesting that these species are potentially manipulated by the parasite. However, to our knowledge, such information is lacking for most fish species infected by *Diplostomum* parasites.

The aim of the present study was to quantify the occurrence of parasite-induced cataracts in fish populations across a natural host community and subsequently assess potential for host manipulation by *Diplostomum* eye flukes in the wild. It is important to note that the taxonomy of these parasites is not completely resolved (see Gibson, 1996; Galazzo *et al.* 2002), and fish are often infected with more than one eye fluke species (e.g. Valtonen and Gibson, 1997; Locke *et al.* 2010). Therefore we refer to *Diplostomum* spp. in this work. By sampling populations of 7 fish species from the Bothnian Bay in the Baltic Sea we found that the parasite-induced cataracts were common in fish and they also reached levels that are likely to predispose fish to predation (see Seppälä *et al.* 2005b). However, we observed intensive cataracts only in species with the highest parasite abundances, which suggests that only certain hosts may be strongly affected by the infection.

## MATERIALS AND METHODS

### Data collection

In May 2006, we sampled 7 fish species, ruffe (*Gymnocephalus cernuus*), roach (*Rutilus rutilus*), dace (*Leuciscus leuciscus*), bleak (*Alburnus alburnus*), smelt (*Osmerus eperlanus*), whitefish (*Coregonus lavaretus*) and three-spined stickleback (*Gasterosteus aculeatus*), 100 individuals of each, from the N.E. Bothnian Bay (65°06'N, 25°19'E) in the Baltic Sea. Studied species are very common in the area and thus potentially important hosts for the parasites. We collected the samples in spring, before the beginning of parasite transmission from snails (see Karvonen

*et al.* 2004b). We did this to ensure that the fish were not infected with any recently established parasites since metacercariae generally induce cataracts after they have reached infectivity to the avian hosts (see Seppälä *et al.* 2005b). We caught the fish using fyke nets and brought them to the laboratory immediately after catching for further examination.

We measured the coverage of parasite-induced cataracts from the lenses of each fish with a Kowa Portable Slit Lamp SL-14 microscope (see Wall and Bjerkås, 1999; Karvonen *et al.* 2004a) using a subjective scale: 0=no cataracts, 1=cataracts covering less than 25%, 2=cataracts covering 25–50%, 3=cataracts covering 50–75%, 4=cataracts covering 75–100%, 5=cataracts covering 100% of the lens horizontal area. We did not estimate 'thickness' of the cataracts. Based on our earlier study on predation vulnerability of infected rainbow trout (*Oncorhynchus mykiss*) (Seppälä *et al.* 2005b), we considered cataracts covering more than 50% of the lens area (mean from both eyes) likely to increase the susceptibility of fish to predation. For the purpose of this study, we considered the effect of cataracts to be similar across the fish species. However, we can not completely rule out the possibility for slight differences in cataract development and degree of manipulation between the fish species, as well as between different *Diplostomum* species possibly occurring in these fish (see Discussion section). Nevertheless, it is important to note that in all studied fish species, development of cataracts in relation to the number of parasites followed the same general pattern. In low-level infections, individual parasites were surrounded by their metabolites, which accumulated with the number of parasites leading to gradual loss of opacity of the lens as the metabolites became overlapping. Furthermore, our goal was not to estimate the exact predation rates of fish, or the mechanisms underlying possible variation in cataract coverage among the host species, but instead to use cataract coverage as a proxy of the potential of host manipulation.

Cataracts induced by factors other than parasites (e.g. nutrition, temperature) can also occur in fish (see Bjerkås and Sveier, 2004). However, we considered this unlikely in the present study because the coverage of the cataracts depended on parasite abundance (number of parasites in a fish; Bush *et al.* 1997) in all studied fish species (Spearman's rank correlation: ruffe:  $r=0.833$ ,  $P<0.001$ ; roach:  $r=0.814$ ,  $P<0.001$ ; dace:  $r=0.739$ ,  $P<0.001$ ; bleak:  $r=0.743$ ,  $P<0.001$ ; smelt:  $r=0.768$ ,  $P<0.001$ ; whitefish:  $r=0.892$ ,  $P<0.001$ ; three-spined stickleback:  $r=0.779$ ,  $P<0.001$ ), and we did not find any cataracts from the uninfected fish individuals. After determining the coverage of cataracts, we dissected the eye lenses to count the *Diplostomum* metacercariae in them, and measured the length of each fish ( $\pm 1$  mm). Since we were only interested in fish suitable in size for avian predation (definitive hosts of the parasites), we did

Table 1. Number of fish studied ( $N$ ), body length, prevalence of infection (%), mean and median abundance of parasites, and estimate of the degree of aggregation of the frequency distribution of parasites ( $k$ ) in seven wild fish populations studied from the N.E. Bothnian Bay in the Baltic Sea

Fish species	$N$	Body length (mm)	Prevalence	Abundance		$k$
		Mean $\pm$ s.e.		Mean	Median	
<i>G. cernuus</i>	98	106 $\pm$ 1.9	100	20.0	19.0	2.90
<i>R. rutilus</i>	98	141 $\pm$ 1.3	100	30.8	23.0	1.82
<i>L. leuciscus</i>	92	160 $\pm$ 1.3	100	79.3	65.0	3.66
<i>A. alburnus</i>	99	130 $\pm$ 1.2	90	4.4	4.0	2.20
<i>O. eperlanus</i>	98	151 $\pm$ 1.5	91	5.6	4.0	1.47
<i>C. lavaretus</i>	86	140 $\pm$ 3.6	70	5.6	2.5	0.51
<i>G. aculeatus</i>	99	64 $\pm$ 0.4	76	2.1	2.0	1.65

not consider fish longer than 200 mm (see Bugoni and Vooren, 2004; Mauco and Favero, 2004). From a total of 30 fish, we could not determine either cataract coverage or parasite abundance and we excluded them from the data.

### Statistical analyses

We analysed the variation in the coverage of parasite-induced cataracts between fish species using a Kruskal-Wallis test. We used a non-parametric test because we measured cataract coverage using an ordinal scale (6 categories; see above). In the analysis, we used the mid-value from both eyes as a response variable. Furthermore, because frequency distributions of most macroparasites are aggregated in the host populations (i.e. most individuals have low parasite abundances, and only few have very high abundances; see Shaw *et al.* 1998), we estimated the degree of aggregation in our study populations using maximum-likelihood methods (see Wilson *et al.* 1996). Since our data showed aggregation in all studied fish populations (Table 1; the distribution converges to Poisson when  $k > 20$  (Wilson *et al.* 1996), we analysed the variation in parasite abundance between the fish species using a generalized linear model (GZLM) with negative binomial errors and log-link function. We also analysed the relationship between parasite abundance and cataract coverage among the fish species using a Spearman's rank correlation. In the analysis, we used the medians of parasite abundance and cataract coverage as variables. We conducted all analyses and distribution fitting using the R 2.8.0 statistical package.

### RESULTS

We found parasite-induced cataracts from all studied fish species (Fig. 1), and the cataract coverage reached high levels (i.e. the mid-coverage of both eyes being at least 50% which potentially predisposes fish to predation (see Seppälä *et al.* 2005b) in 13% of the studied fish individuals. However, the coverage of cataracts varied between the fish species

(Kruskal-Wallis test:  $\chi^2_6 = 379.46$ ,  $P < 0.001$ ; Fig. 1), and we observed intensive cataracts (>50% coverage) only in dace (66% of individuals), ruffe (14% of individuals) and roach (11% of individuals). Furthermore, the abundance of infection between the fish species was highly variable (GZLM: estimate = 0.20, s.e. = 0.03,  $Z = 7.71$ ,  $P < 0.001$ ), mean and median abundances ranging from 2.1 and 2.0 in three-spined stickleback to 79.3 and 65.0 in dace, respectively (Table 1). The rank correlation between parasite abundance and cataract coverage (medians) was positive among the fish species (Spearman's rank correlation:  $r = 0.898$ ,  $P = 0.006$ ), which suggests that the between-species variation in the coverage of parasite-induced cataracts was at least partly determined by variation in parasite abundance.

### DISCUSSION

Trophically transmitted parasites commonly increase their transmission probability by manipulating their intermediate hosts' phenotype in ways which predispose them to predation (reviewed by Moore, 2002). *Diplostomum* eye flukes are also known to alter fish behaviour (Crowden and Broom, 1980; Seppälä *et al.* 2004, 2008b) and appearance (Seppälä *et al.* 2005a) so that their vulnerability to predation increases (Seppälä *et al.* 2004, 2005b). The most likely mechanism leading to host manipulation in this system is cataract formation induced by the parasites (Seppälä *et al.* 2005b). However, the formation of parasite-induced cataracts and host manipulation have been described in detail only under laboratory conditions using farmed rainbow trout as a model host species (Seppälä *et al.* 2005b). Thus, the occurrence of cataracts and the subsequent potential for host manipulation in natural host populations have remained largely unknown (but see Marcogliese *et al.* 2001). In this study, we found that the parasite-induced cataracts are common in natural fish populations, and they can reach levels which potentially predispose fish to predation (>50% coverage; see Seppälä *et al.* 2005b). This suggests that *Diplostomum*

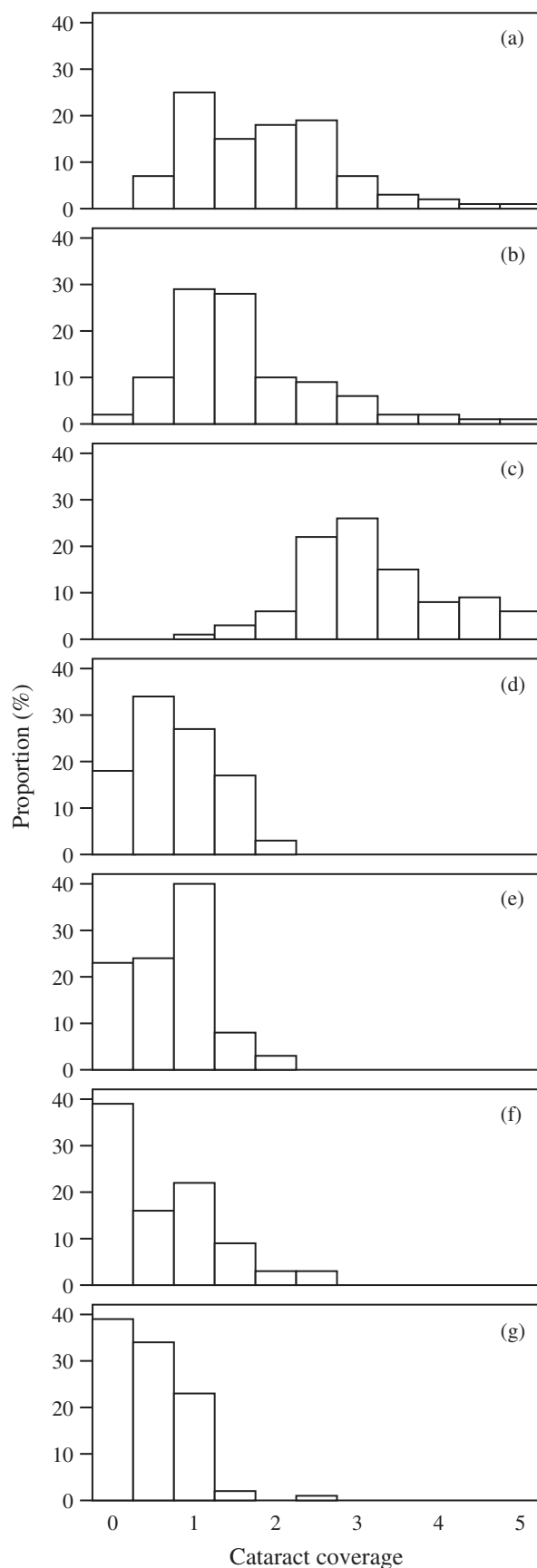


Fig. 1. Frequency distributions (proportions) of parasite-induced cataracts observed in eye lenses of (a) *G. cernuus*, (b) *R. rutilus*, (c) *L. leuciscus*, (d) *A. alburnus*, (e) *O. eperlanus*, (f) *C. lavaretus* and (g) *G. aculeatus* studied from N.E. Bothnian Bay in the Baltic Sea.

parasites are likely to manipulate their fish hosts in nature.

Although parasite-induced cataracts were common in the studied fish populations, the coverage of cataracts varied greatly between the fish species. We found intensive cataracts (>50% coverage) only in dace (66% of individuals), ruffe (14% of individuals) and roach (11% of individuals), which suggests that only certain species may be strongly affected by the infection. It is important to note, however, that we did not measure the susceptibility of fish to predation directly, but estimated the potential for host manipulation in terms of cataract coverage. Thus, the effect of the infection on actual predation rates can be different if, for instance, the effect of cataracts in different species is not similar. For example, species preferring shallow waters, such as dace and roach, are likely to be exposed to avian predation more frequently than benthic fish such as ruffe. This is because many bird species, such as gulls and terns, are able to catch fish only from the water surface whereas diving birds, such as loons and mergansers, can reach also deeper water layers. Therefore, possible increase in the susceptibility to predation due to cataracts is likely to depend also on host ecology. Furthermore, because we sampled natural fish populations, it is possible that individuals with the highest coverage of cataracts were under-represented in the samples if, in general, they are rapidly removed from the populations by predators (see Seppälä *et al.* 2005b). This could mean that the species with the lowest observed cataract coverage (<25% of the lens area; bleak, smelt, whitefish, three-spined stickleback) were actually the most strongly manipulated. This, however, is unlikely because the intermediate cataract intensities (i.e. 25–50% coverage), below the proposed ‘threshold’ of manipulation (50% coverage; Seppälä *et al.* 2005b), were mostly missing in those species.

The coverage of cataracts also depended on parasite abundance so that we found intensive cataracts (>50% coverage) only from the species with the highest parasite abundances (dace, roach and ruffe). This suggests that the abundance of infection at least partly explains the observed differences in the coverage of parasite-induced cataracts among the fish species (see also Karvonen *et al.* 2004a). Thus, factors underlying variation in parasite abundance likely contribute also to variation in cataract formation. However, also other factors may be important. For example, as we did not determine the parasite species identity in the studied fish populations, the

The coverage of cataracts was measured using a subjective scale: 0 = no cataracts, 1 = cataracts covering less than 25%, 2 = cataracts covering 25–50%, 3 = cataracts covering 50–75%, 4 = cataracts covering 75–100%, 5 = cataracts covering 100% of the lens horizontal area. The mid-values of both eyes are shown in the figure.

fish may have been infected with different eye fluke species (see Locke *et al.* 2010). This may have brought some additional variation in cataract formation among the fish species. However, *Diplostomum* species infecting fish eye lenses are ecologically (e.g. life cycle, transmission strategies) very similar. Thus, their ability to induce cataracts can be expected to be under similar selective pressures, and the differences among species are likely to be small. Furthermore, it is possible that fish species differ in their susceptibility to cataract formation, i.e. a certain abundance of infection may induce different coverage of cataracts in different species. This is possible, for example, because the size of the lens varies considerably between fish species (Karvonen and Seppälä, 2008), and the number of parasites required to impair fish vision is likely to increase with lens size. This suggests that the species with the smallest lenses could be most vulnerable to reduction in vision due to the infection. This question, however, could not be addressed using these data and would require controlled experimental infections of uninfected individuals under laboratory conditions. However, techniques for the production and maintenance of several wild fish species under parasite-free laboratory conditions are currently not available.

To conclude, our results show that *Diplostomum* parasites are able to induce high-level cataracts in the wild populations of their natural fish hosts. This supports the earlier conclusions from laboratory experiments by suggesting that eye flukes are likely to manipulate fish phenotype also under natural conditions. Potential for manipulation, however, may vary among host species because intensive cataracts were observed only in certain fish species. Thus, different host species may not be equally affected by the infection and only some of them may be primarily responsible for maintaining the parasite populations ('required hosts'; *sensu* Holmes, 1979). Furthermore, such variation could be reflected in parasite population dynamics and even energy flow in natural food webs, which is why manipulation could also have wider implications at the ecosystem level (see Lefèvre *et al.* 2009). These questions, however, remain to be investigated.

#### ACKNOWLEDGEMENTS

We thank R. Halonen, P. Rintamäki and T. Valtonen for help in providing the fish, and anonymous reviewers for their comments on the manuscript. The study was funded by Emil Aaltonen Foundation (O.S.), Kone Foundation (O.S.), and the Academy of Finland (O.S., A.K.).

#### REFERENCES

- Bethel, W. M. and Holmes, J. C. (1973). Altered evasive behaviour and responses to light in amphipods harboring acanthocephalan cystacanths. *Journal of Parasitology* **59**, 945–956.
- Bethel, W. M. and Holmes, J. C. (1977). Increased vulnerability of amphipods to predation owing to altered behaviour induced by larval acanthocephalans. *Canadian Journal of Zoology* **55**, 110–115.
- Bjerkås, E. and Sveier, H. (2004). The influence of nutritional and environmental factors on osmoregulation and cataracts in Atlantic salmon (*Salmo salar* L). *Aquaculture* **235**, 101–122.
- Bugoni, L. and Vooren, C. M. (2004). Feeding ecology of the Common Tern *Sterna hirundo* in a wintering area in southern Brazil. *Ibis* **146**, 438–453.
- Bush, A. O., Lafferty, K. D., Lotz, J. M. and Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.
- Crowden, A. E. and Broom, D. M. (1980). Effects of eyefluke, *Diplostomum spathaceum*, on the behaviour of dace (*Leuciscus leuciscus*). *Animal Behaviour* **28**, 287–294.
- Galazzo, D. E., Dayanandan, D., Marcogliese, D. J. and McLaughlin, J. D. (2002). Molecular systematics of some North American species of *Diplostomum* (Digenea) based on rDNA sequence data and comparisons with European congeners. *Canadian Journal of Zoology* **80**, 2207–2217.
- Gibson, D. I. (1996). Trematoda. In *Guide to the Parasites of Fishes of Canada, Part IV* (ed. Margolis, L. and Kabata, Z.), pp. 1–373. Canadian Special Publication of Fisheries and Aquatic Sciences No. 124. NRC Press, Ottawa, Canada.
- Holmes, J. C. (1979). Parasite populations and host community structure. In *Host–Parasite Interfaces* (ed. Nickol, B. B.), pp. 27–46. Academic Press, London, UK.
- Holmes, J. C. and Bethel, W. M. (1972). Modification of intermediate host behaviour by parasites. In *Behavioural Aspects of Parasite Transmission* (ed. Canning, E. U. and Wright, C. A.), pp. 123–149. Academic Press, London, UK.
- Karvonen, A. and Seppälä, O. (2008). Eye fluke infection and lens size reduction in fish: a quantitative analysis. *Diseases of Aquatic Organisms* **80**, 21–26.
- Karvonen, A., Seppälä, O. and Valtonen, E. T. (2004a). Eye fluke-induced cataract formation in fish: quantitative analysis using an ophthalmological microscope. *Parasitology* **129**, 473–478.
- Karvonen, A., Seppälä, O. and Valtonen, E. T. (2004b). Parasite resistance and avoidance behaviour in preventing eye fluke infections in fish. *Parasitology* **129**, 159–164.
- Lagrange, C., Kaldonski, N., Perrot-Minnot, M. J., Motreuil, S. and Bollache, L. (2007). Modification of hosts' behaviour by a parasite: field evidence for adaptive manipulation. *Ecology* **88**, 2839–2847.
- Lafferty, K. D. and Morris, K. (1996). Altered behaviour of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* **77**, 1390–1397.
- Lefèvre, T., Lebarbenchon, C., Gauthier-Clerc, M., Misse, D., Poulin, R. and Thomas, F. (2009). The ecological significance of manipulative parasites. *Trends in Ecology and Evolution* **24**, 41–48.
- Locke, S. A., McLaughlin, J. D., Dayanandan, S. and Marcogliese, D. J. (2010). Diversity and specificity in *Diplostomum* spp. metacercariae in freshwater fishes revealed by cytochrome *c* oxidase I and internal

- transcribed spacer sequences. *International Journal for Parasitology* **40**, 333–343.
- Marcogliese, D. J., Dumont, P., Gendron, A. D., Mailhot, Y., Bergeron, E. and McLaughlin, J. D.** (2001). Spatial and temporal variation in abundance of *Diplostomum* spp. in walleye (*Stizostedion vitreum*) and white suckers (*Catostomus commersoni*) from the St. Lawrence River. *Canadian Journal of Zoology* **79**, 355–369.
- Mauco, L. and Favero, M.** (2004). Diet of the common tern (*Sterna hirundo*) during the nonbreeding season in Mar Chiquita Lagoon, Buenos Aires, Argentina. *Ornitologia Neotropical* **15**, 121–131.
- Moore, J.** (1983). Responses of an avian predator and its isopod prey to an acanthocephalan parasite. *Ecology* **64**, 1000–1015.
- Moore, J.** (2002). *Parasites and the Behaviour of Animals*. Oxford University Press, Oxford, UK.
- Mouritsen, K. M. and Poulin, R.** (2003). Parasite-induced trophic facilitation exploited by a non-host predator: a manipulator's nightmare. *International Journal for Parasitology* **33**, 1043–1050.
- Rothschild, M.** (1962). Changes in behaviour in the intermediate hosts of trematodes. *Nature, London* **193**, 1312–1313.
- Rushton, W.** (1937). Blindness in freshwater fish. *Nature, London* **140**, 1014.
- Rushton, W.** (1938). Blindness in freshwater fishes. *Nature, London* **141**, 289.
- Shaw, D. J., Grenfell, B. T. and Dobson, A. P.** (1998). Patterns of macroparasite aggregation in wildlife host populations. *Parasitology* **177**, 597–610.
- Seppälä, O., Karvonen, A. and Valtonen, E. T.** (2004). Parasite-induced change in host behaviour and susceptibility to predation in an eye fluke–fish interaction. *Animal Behaviour* **68**, 257–263.
- Seppälä, O., Karvonen, A. and Valtonen, E. T.** (2005a). Impaired crypsis of fish infected with a trophically transmitted parasite. *Animal Behaviour* **70**, 895–900.
- Seppälä, O., Karvonen, A. and Valtonen, E. T.** (2005b). Manipulation of fish host by eye flukes in relation to cataract formation and parasite infectivity. *Animal Behaviour* **70**, 889–894.
- Seppälä, O., Karvonen, A. and Valtonen, E. T.** (2008b). Shoaling behaviour of fish under parasitism and predation risk. *Animal Behaviour* **75**, 145–150.
- Seppälä, O., Valtonen, E. T. and Benesh, D. P.** (2008a). Host manipulation by parasites in the world of dead-end predators: adaptation to enhance transmission? *Proceedings of the Royal Society of London, B* **275**, 1611–1615.
- Valtonen, E. T. and Gibson, D. I.** (1997). Aspects of the biology of diplostomid metacercarial (Digenea) populations occurring in fishes in different localities of northern Finland. *Annales Zoologici Fennici* **34**, 47–59.
- Wall, T. and Bjerkås, E.** (1999). A simplified method of scoring cataracts in fish. *Bulletin of the European Association of Fish Pathologists* **19**, 162–165.
- Wilson, K., Grenfell, B. T. and Shaw, D. J.** (1996). Analysis of aggregated parasite distribution: a comparison of methods. *Functional Ecology* **10**, 592–601.