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REVIEW

Treatment of gyrodactylid infections in fish

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ABSTRACT: Since Norway experienced the devastating *Gyrodactylus salaris* (Monogenea) epidemics in Atlantic salmon *Salmo salar*, there has been heightened interest in how to treat gyrodactylosis in fish. Here we summarize chemical treatments previously used against gyrodactylids and discuss the main problems associated with these control measures including efficacy, host toxicity, human health concerns and application of treatments. Unfortunately, for these reasons and because of the different methodologies and different parasite and host species used in previous studies, it is difficult to recommend effective chemotherapeutic treatments. However, we suggest a method for manual removal of gyrodactylids from the host suitable for use in small-scale research facilities.

KEY WORDS: *Gyrodactylus* · Control treatment · Efficacy · Toxicity

INTRODUCTION

A frequently asked, but rarely addressed, question is what is the most effective means of removing *Gyrodactylus* spp. from their hosts? With increasing interest in this large group of ectoparasitic worms, not only as important pathogens but also as model organisms (reviewed by Bakke et al. 2002, 2007, Cable & Harris 2002), it seems timely to document the methods that have been used thus far to remove gyrodactylids.

PROBLEMS WITH EXISTING TREATMENTS

Appendix 1 lists 88 compounds and treatment combinations that have previously been used to treat gyrodactylid infections in research facilities, aquaculture and the hobbyist market. However, selecting the best of these treatments is difficult, because few studies have compared compounds using the same methodologies and the majority of treatments have various associated problems. Formaldehyde, for instance, was found to be 100% effective at eliminating *Gyrodactylus salaris* experimentally (Buchmann & Kristensson 2003), but under large-scale aquaculture conditions it does not eradicate gyrodactylids completely (Rintamäki-Kinnunen & Valtonen 1996, Rowland et al. 2006), and in some three-spined stickleback *Gasterosteus aculeatus* populations it is only 10% effective (J. Cable pers. obs.). Due to its broad anti-parasitic properties, formaldehyde is still commonly used in aquaculture, even though it is classed as a human carcinogen (IARC 2004). Mutagenic and carcinogenic effects are also known for malachite green (Srivastava et al. 2004), which like formaldehyde is widely used as an anti-parasitic treatment, but its effectiveness against *Gyrodactylus* spp. has not been evaluated. Malachite green is now banned in food fish production in Europe and North America as it is retained in fish flesh (European Council 1990; US Food and Drug Administration and the Canadian Food Inspection Agency, cited in Srivastava et al. 2004).

Alternative treatments include rotenone, an indiscriminate ATPase inhibitor which has been used to control *Gyrodactylus salaris* in Norway by killing all potential hosts (reviewed in Bakke et al. 2007), including other gill-breathing organisms. This is only partially effective and has potential negative effects on human health. Aqueous aluminium is another alternative that is being tested. However, although aluminium ap-

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peared promising in laboratory studies (Soleng et al. 1999, 2005, Poléo et al. 2004), field trials in Norway using aluminium in combination with rotenone have been problematic because successful treatment of the whole river system requires maintaining a specific concentration without exceeding levels toxic to Atlantic salmon (P. Shave pers. comm.). Aluminium toxicity to fish increases under acidic water conditions (Birchall et al. 1989, Poléo 1995, Soleng et al. 1999), and elevated environmental aluminium levels can result in Alzheimer's disease (Doll 1993) and decreased agricultural and forestry productivity (Bi et al. 2001). Organophosphates, such as trichlorfon, are no longer in use against fish parasites as they cause irreversible effects in non-target species by phosphorylating acetylcholinesterase (see Kozlovskaya & Mayer 1984, Peña-Llopis et al. 2003, Costa 2006). Acute and chronic toxicity to other aquatic organisms has also been reported for benzimidazoles (e.g. Oh et al. 2006); however, due to their low efficacy (see Appendix 1), these are not preferred over broad antiparasitic treatments such as formalin.

In addition to efficacy, environmental and human health issues, the main problem associated with current gyrodactylid treatments is their toxicity to the host (Schmahl & Taraschewski 1987, Santamarina et al. 1991, Tojo et al. 1992, Scholz 1999, Ekanem et al. 2004, Srivastava et al. 2004). Even widely used compounds, such as formaldehyde, may significantly change the host's gill structure and epidermis (Speare et al. 1997, Sanchez et al. 1998, Buchmann et al. 2004). For instance, although zinc exposure initially stimulates host mucus production, mucus is subsequently depleted leaving the fish more susceptible to microbial infections (McGeer et al. 2000). If these fish are subsequently used for experimental infections without a sufficient recovery period, they may show an abnormal response to infection (see review by Bakke et al. 2007). Host respiratory problems are also a common side effect of gyrodactylid treatments due to direct interference with gill function and indirectly via reduction of water quality (e.g. decrease in pH and/or dissolved oxygen: Smith & Piper 1972, Ross et al. 1985, Rowland et al. 2006). Toxicity in many cases is dose-dependent, but may also be affected by one or a combination of the following factors: temperature, pH, salinity, mechanism of delivery, species and exposure time (Schmahl & Taraschewski 1987, Schmahl et al. 1989, Scholz 1999), especially where multiple treatments are used.

Gyrodactylid treatments are applied either orally (with food) or topically (added to the water). Both methods usually lead to application of overly high doses to compensate for lack of control over drug administration (Scholz 1999), which may lead to environmental contamination. Oral administration of some drugs can also reduce host food consumption (e.g. piperazine, Fugotenil® and Neguvon®; Tojo & Santamarina 1998), which increases the dosage needed per unit of food for efficacy. Additionally, compounds that are partially effective as baths may not be effective if administered orally (e.g. trichlorfon; Santamarina et al. 1991, Tojo & Santamarina 1998). Moreover, resistance of parasites against antihelminthics has been reported, with Goven & Amend (1982) and Schmahl et al. (1989) finding resistance of gyrodactylids to dimethyl phosphonate and trichlorfon, respectively. Breeding parasite-resistant fish or developing a vaccine against gyrodactylosis would override many of the above problems and bypass the potential issue of drug resistance. Breeding experiments with wild Atlantic salmon *Salmo salar* that show resistance against *Gyrodactylus salaris* are currently under way in Norway (R. Salte et al. unpubl.), but we are unaware of any plans for vaccine development. In Norway destocking and drying of fish farms was used successfully to eradicate *G. salaris* (see Mo 1994); however, this method is not suitable for establishments which receive potentially infected fish on a regular basis and infected fish would still have to be treated.

A major problem with many of the studies presented in Appendix 1 is that they used sub-sampling methods, such as mucus scrapings (e.g. Tojo et al. 1992, Tojo & Santamarina 1998) or partial examination of fish populations in field trials (e.g. Goven & Amend 1982). This is a crude and unreliable estimate of parasite infection, particularly where the gyrodactylid is not identified to species level (e.g. Tojo & Santamarina 1998, Chansue 2007) as different *Gyrodactylus* spp. show marked site specificities. Furthermore, the majority of compounds trialled successfully have been tested only once. For those with at least 2 independent studies, results have been variable probably because of different methodologies. Hence, many seemingly successful compounds may not be effective when it comes to treating a different host–parasite system. Field studies are of particular importance as they provide an indication of how efficient treatments are on a large scale, potentially for use in the ornamental or food fish industries. However, there have only been a few such studies (see Appendix 1) with only Rach et al. (2000) claiming 100% efficiency for the compound they tested (hydrogen peroxide). Other authors defined a treatment in the field as successful if it just reduced the pathogen burden (e.g. Lewis 1967, Rintamäki-Kinnunen & Valtonen 1996).

MANUAL REMOVAL OF GYRODACTYLIDS

Due to toxicity and/or difficulties in administration (such as the need for prolonged exposure), no treat-

ment detailed in Table 1 is entirely satisfactory or 100% effective, although several treatments indicate 100% efficacy against gyrodactylosis (e.g. formaldehyde and aqueous aluminium). In laboratory trials with small, hardy fish, the most effective means of removing gyrodactylids (at least those that predominantly occur on the skin and fins) is a licensed Home Office procedure in the UK which requires the host to be lightly anaesthetised (using e.g. 0.02% MS-222, chlorobutanel) whilst the living parasites are removed manually. Following anaesthesia, the fish is transferred to a shallow dish, but kept fully immersed in dechlorinated water and screened using a stereo-microscope with fibre-optic illumination. The latter is essential to prevent the host and parasites overheating during examination on the microscope stage. Parasites can be most easily detected by their movement, but it is still essential to scan all surfaces of the host. Small fish, such as guppies and sticklebacks, can be manipulated using a plastic disposable pipette tip. Once a parasite is detected, the worm can be removed and crushed using watchmaker's forceps. It is essential to ensure that the parasite is not released directly back into the water as even a damaged worm may re-attach to its host and successfully give birth. Once all parasites have been removed, the same screening procedure should be repeated until all fish in a population have been screened clear of parasites on 3 consecutive occasions separated by approximately 1 wk, ideally by 2 independent, trained researchers. If a parasite is found on any fish during this process, then the screening process should begin again for the entire host population.

For small fish, such as poeciliids, manual removal of parasites can be effective without any chemical intervention. However, for larger fish (or where gyrodactylids are abundant and/or show a preference for the gills), chemical treatment prior to screening may be the only practical solution to parasite removal. In our laboratories we use levamisole, but this is only available by veterinarian prescription and only reliable if applied to single fish that are closely monitored for signs of toxicity. Screening is still essential to ensure that fish are free of gyrodactylids following chemical treatment, with additional screening on subsequent occasions to ensure the experimental fish are free from infection. For larger fish, such as adult Atlantic salmon *Salmo salar*, sub-sampling by examining mucus scrapings or selected fins may be the only practical way of screening, but this is not accurate. It is also stressful for the fish as it damages the fish's epithelium, so increasing the risk of secondary infections. An alternative or ideally supplementary procedure to manual removal, but again only suitable for small fish, is to maintain each fish in isolation in a closed system with regular water changes. As fish become immune and gyrodactylids are shed, there is no opportunity for the parasites to transfer to new hosts. However, even long periods of isolation are not always effective for certain host–parasite combinations (see King et al. 2008) and the accompanying high maintenance is extremely time consuming and costly. Whatever the control method used (chemical, manual or host isolation), thorough screening is essential to ensure parasite extinction. The longer the interval between the 3 consecutive screens the more reliable the procedure. A single (transparent, <1 mm long) gyrodactylid missed in an earlier screen will have had ample time to reproduce *in situ* (as little as 24 h at 25°C) generating a larger number of parasites which are less likely to be overlooked on subsequent screens.

CONCLUSION

Although the majority of compounds tested against *Gyrodactylus* spp. are reportedly effective (see Appendix 1), 100% efficacy has not been achieved without toxicity to hosts. Currently, the lack of comparative data makes the selection of a drug difficult. Leaving just one (hermaphrodite, viviparous) worm can be sufficient to initiate a new disease outbreak. For research projects, manual removal of skin gyrodactylids from small fish is an option; however, this is not feasible for gill parasites, larger hosts or for use in aquaculture. Further research into different treatments and their application on different species of parasite and host is necessary to combat the existing problems caused by *Gyrodactylus* spp. epizootics.

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Appendix 1. Treatments against infections of *Gyrodactylus* species. With the exception of orally administered treatments, other compounds below were applied directly to the water

Compound	Dose	Application	*Gyrodactylus* spp.	Host	Efficacy	Source
(1) Botanicals						
Rotenone	Used extensively to treat *G. salaris* on salmonids in Norwegian rivers. Kills both fish and parasites. Linked to Parkinson's disease.[a]					Pesticide Action Network UK (2001), Harris et al. (2008), Caboni et al. (2004)
Terminalia catappa extract	1.7, 3.4 & 5.1 g l^{-1}	4 wk. Lab study	*Gyrodactylus* sp.	*Carassius auratus*	Not effective (1.7 g l^{-1}) to 100% effective after 14 d (5.1 g l^{-1})[b]	Chansue (2007)
Tea tree oil and Tween 80	3, 10 & 30 ppmv in 0.01% Tween	48 h. 13°C. Lab study	*Gyrodactylus* spp. (probably *G. gasterostei* and/or *G. arcuatus*)	*Gasterosteus aculeatus*	Reduced parasite mean from 12.6 worms $fish^{-1}$ to 1.4 (30 ppmv)[b]	Steverding et al. (2005)
	0.01% Tween				Reduced parasite mean from 12.6 worm $fish^{-1}$ and reduced prevalence by 45%[b]	
Piper guineense extract	0.5, 1.0, 1.5 & 2 mg l^{-1}	96 h. Test solution renewed every 24 h. Lab study	*G. elegans*	*Carassius auratus auratus* (10 fish $treatment^{-1}$)	Dose dependent, but none 100% effective[a,b,c]	Ekanem et al. (2004)
(2) General chemotherapeutics						
Acaprin (Acaprina®)	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	96% effective[d,e]	Tojo et al. (1993a)
Agerin®	10, 500 & 1000 ppm	Indefinite time, 2 & 1 h, respectively. 18°C. Lab study	*Gyrodactylus* sp.	*Oreochromis niloticus*	Not effective[c]	El-Khatib (2003)
Albendazole (Oversol®)	25 & 200 mg l^{-1}	12 & 3 h, respectively. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective (200 mg l^{-1}) to 95.5% effective (25 mg l^{-1})[a,d,e]	Tojo et al. (1992)
Aminosidine (Gabbrocol®)	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Aminosidine (Gabroral®)	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993a)
Amprolium (Prolsal®)	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993a)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Benznidazole	200 mg l^{-1}	3 h. 11°C. Lab. study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993a)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Bithionol	4, 20 & 60 mg l^{-1}	3 h. 15°C. Lab. study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish $treatment^{-1}$)	98.6% effective (4 mg l^{-1}) to 100% effective (20 & 60 mg l^{-1}) [a,d,e]	Santamarina et al. (1991)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Carnidazole (Spartrix®)	10 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993a)
Chloroquine	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Chloroquine diphosphate	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993a)
Closantel (Flukiver®)	0.25 & 0.125 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish $treatment^{-1}$)	99.6% effective (0.125 mg l^{-1}) to 100% effective (0.25 mg l^{-1})[a,d,e]	Santamarina et al. (1991)

Appendix 1 (continued)

Compound	Dose	Application	*Gyrodactylus* spp.	Host	Efficacy	Source
Diethylcarbamazine	200 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective[e]	Tojo et al. (1993b)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish treatment^{-1})	Not effective[f]	Tojo & Santamarina (1998)
Dimetridazole	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective[e]	Tojo et al. (1993a)
Diminazene aceturate (Berenil®)	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	98.6% effective[d,e]	Tojo et al. (1993a)
Febantel (Rintal®)	2 & 10 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish treatment^{-1})	Not effective (2 mg l^{-1}) to toxic to host (10 mg l^{-1}: 4 trout dead after 1 h, expt. terminated)[a,d,e]	Santamarina et al. (1991)
Fenbendazole (Panacur®)	0.77, 1.5, 6.2, 12.5 & 25 mg l^{-1}	12 h (additionally, 3 h for 25 mg l^{-1}) 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective (0.77 mg l^{-1} & 25 mg l^{-1} for 3 h) to 100% effective (>1.5 mg l^{-1})[a,d,e]	Tojo et al. (1992)
Flubendazole	25 & 200 mg l^{-1}	12 & 3 h, respectively. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective[a,e]	Tojo et al. (1992)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish treatment^{-1})	Not effective[e]	Tojo & Santamarina (1998)
Formaldehyde	2.5, 5, 10, 20, 40 & 60 mg l^{-1}	18 h. Lab study	*G. aculeati*	*Gasterosteus aculeatus*	Not effective (2.5 mg l^{-1}) to 100% effective (20, 40 & 60 mg l^{-1})[g]	Buchmann & Kristensson (2003)
Formalin	20, 25, 30 & 40 mg l^{-1}	24.1–26.9°C or 13.2–15.7°C. Field trial: applied to ponds	*Gyrodactylus* sp.	*Bidyanus bidyanys*	Not effective (20, 25 mg l^{-1}) to sig. decrease (30, 40 mg l^{-1})[b,c]	Rowland et al. (2006)
Formalin; malachite green & formalin; salt bath	0.2 g l^{-1}; 4 g l^{-1} & 0.2 g l^{-1}; 1.5–2%, respectively	Farm study: rotation of treatments	Putatively *G. salaris*	*Salmo salar, S. trutta trutta & S. t. lacustris*	Formalin partially effective (decreased parasite burden); malachite green + formalin, and/or salt not effective[b,g]	Rintamäki-Kinnunen & Valtonen (1996)
Formalin (For) & malachite green (MG)	Recommended use in combination: 3.68 g MG in 1 l For, used at 0.025 ml l^{-1} of water for 60 min, or 3.3 g MG in 1 l For used at 0.015 ml l^{-1} of water as a prolonged immersion. Synergistic effect of compounds in combination, but toxic to both parasite and host					Srivastava et al. (2004), Fishdoc (2008)
HOE 092 V (triazine derivative)	0, 2, 5, 10 & 15 µg l^{-1}	1, 2, 3 & 4 h. 22°C. Lab study	*G. arcuatus*	*Gasterosteus aculeatus*	Not effective (0–5 µg l^{-1}) to effective after 4 h (10 µg l^{-1}) & 1 h (15 µg l^{-1})[a,b,c]	Schmahl (1993a)
	10 mg l^{-1}	3 h	*G. groschaffi*		Effective[h]	Cited in: Schmahl (1993b)
Hydrogen peroxide	170, 280 & 560 mg l^{-1}	3 × 30 min over 5 d. Field trials	*Gyrodactylus* sp.	*Oncorhynchus mykiss*	100% effective[b,c]	Rach et al. (2000)
	11 & 16 mg l^{-1}; 3 & 6 mg l^{-1}	1 h; 24 h. 23.5°C. Lab study	*Gyrodactylus* spp.	*Xiphophorus helleri* (51–75 fish treatment^{-1})	Not effective[b,c]	Russo et al. (2007)
Ivermectin (Ivomec®)	0.031 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish treatment^{-1})	100% host mortality[a,c,e]	Santamarina et al. (1991)
	0.1 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	96% effective[d,e]	Tojo et al. (1993b)
Ivermectin + clorsulon (Ivomec-F®)	0.025, 0.25, 0.05 & 0.5 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish treatment^{-1})	59% effective (0.025 & 0.25 mg l^{-1}) to 100% effective (0.05 & 0.5 mg l^{-1})[a,d,e]	Santamarina et al. (1991)
Ketoconazole	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective[e]	Tojo et al. (1993a)

Appendix 1 (continued)

Compound	Dose	Application	*Gyrodactylus* spp.	Host	Efficacy	Source
Levamisol hydrochloride	0, 10, 20, 50 & 100 µg l^{-1}	25, 30, 60, 90 & 120 min. 20°C. Lab study	*G. aculeati*	*Gasterosteus aculeatus* (10 fish treatment^{-1})	Decrease of parasite burden[b,c]	Schmahl & Taraschewski (1987)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish treatment^{-1})	Not effective[f]	Tojo & Santamarina (1998)
Levamisol hydrochloride (Citarin-L®)	100 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish treatment^{-1})	Not effective[a,e]	Santamarina et al. (1991)
Malachite green	Recommended use: 0.5–0.8 ppm for 1 d, or 0.015 ppm for prolonged immersion. Remains in fish tissue for up to 1 mo. Highly toxic to fish: carcinogenic, mutagenic, chromosomal fractures, teratogenicity and respiratory toxicity. Now banned in the Europe and N. America for food fish. Most effective used together with formalin.[a]					Kou et al. (1988), Liao et al. (1996), Srivastava et al. (2004)
Mebendazole	0.1 mg l^{-1}	24 h. 23°C. Lab study	*G. elegans*	*Carassius auratus* (10 fish treatment^{-1})	100% effective[b,c]	Goven & Amend (1982)
	25 & 100 mg l^{-1}	12 & 3 h, respectively. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective (100 mg l^{-1}) to 95% effective (25 mg l^{-1})[a,e]	Tojo et al. (1992)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish treatment^{-1})	Not effective[f]	Tojo & Santamarina (1998)
	1 mg l^{-1}	24 h	*G. bullatarudis*		Effective[g,h]	Cited in: Schmahl (1993b)
	0.01 mg l^{-1}	24 h	*G. elegans*		Effective[g,h]	Cited in: Schmahl (1993b)
Mebendazole (Meb) & trichlorfon (Tri)	0.1–0.4 mg l^{-1} Meb & 0.46–1.8 mg l^{-1} Tri	Field tests.	*G. elegans*	*Carassius auratus* (10 fish treatment^{-1})	100% effective[b,c]	Goven & Amend (1982)
	0.5 mg l^{-1} Meb & 2.3 mg l^{-1} Tri	24 h. 23°C. Lab study		*Carassius auratus*, *Astronotus ocellatus*, *Pterphyllum scalare*, *Poecela velifera* & *Trichogaster trichopterus*	100% effective[b,c]	
Meglumine (Glucantime®)	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective[e]	Tojo et al. (1993a)
Methylene blue	Recommendations: 8–10 ppm, bath 1 d; 2 ppm, bath 3–5 d. Highly toxic to fish. Remains in fish tissue for up to 1 mo. Carcinogenic[a]					Liao et al. (1996)
Metronidazole	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective[e]	Tojo et al. (1993a)
Metronidazole (Flagyl®)	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish treatment^{-1})	Not effective[f]	Tojo & Santamarina (1998)
Naftalofos (Maretin®)	20 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective[d,e]	Tojo et al. (1993b)
Netobimin (Hapasil®)	2 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish treatment^{-1})	Not effective[a,e]	Santamarina et al. (1991)
Niclofolan (Bilevon®)	0.025, 0.05 & 0.2 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish treatment^{-1})	91% effective (0.025 mg l^{-1}) to 100% effective (0.05 & 0.2 mg l^{-1}, but all host fish dead)[a,c,e]	Santamarina et al. (1991)
Niclosamide	0, 0.05, 0.075 & 0.1 µg l^{-1}	30, 60, 90 & 120 min. 20°C. Lab study	*G. aculeati*	*Gasterosteus aculeatus* (10 fish treatment^{-1})	Reduction of parasite burden[b]	Schmahl & Taraschewski (1987)
Niclosamide (Fugotenil®)	6 & 1.5 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	100% effective[d,e]	Tojo et al. (1993b)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish treatment^{-1})	Not 100% effective[f]	Tojo & Santamarina (1998)
Niridazole (Ambilhar®)	100 & 200 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish treatment^{-1})	Not effective (100 mg l^{-1}) to 100% effective (200 mg l^{-1})[e]	Tojo et al. (1993b)

Appendix 1 (continued)

Compound	Dose	Application	*Gyrodactylus* spp.	Host	Efficacy	Source
Nitroscanate (Lopatol 500®)	40, 6.25, 0.63, 6.25 g kg^{-1} feed	10 d, 2 d, 1 d, 1 d oral treatment, respectively. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	100% effective[f]	Tojo & Santamarina (1998)
Nitroscanate (Lopatol®)	0.04, 0.07 & 156.25 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish $treatment^{-1}$)	99% effective (0.04 mg l^{-1}) to 100% effective (0.07, 156.25 mg l^{-1})[a,e]	Santamarina et al. (1991)
Nitroxynil (Distomicine®)	30 & 50 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective (30 mg l^{-1}) to 100% effective (50 mg l^{-1})[d,e]	Tojo et al. (1993b)
Nitroxynil	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Oxfendazole	25 & 200 mg l^{-1}	3 h. 15°C. Lab. study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[a,e]	Tojo et al. (1992)
Oxibendazole	25 & 200 mg l^{-1}	12 & 3 h, respectively. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective (200 mg l^{-1}, 3 h) to 86% effective (25 mg l^{-1}, 12 h)[a,d,e]	Tojo et al. (1992)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Paraformaldehyde	Ca. 10 g l^{-1}	Field trial: ponds sized 0.1–0.5 acre (0.04–0.2 ha), ~3 ft (1 m) deep	*G. elegans*	*Notemigonus crysoleucas*	Treatment was successful[b,g]	Lewis (1967)
Parbendazole	25 & 200 mg l^{-1}	12 & 3 h, respectively. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective (200 mg l^{-1}, 3 h) to 91% effective (25 mg l^{-1}, 12 h)[a,e]	Tojo et al. (1992)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Piperazine	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Piperazine citrate	200 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish $treatment^{-1}$)	Not effective[a,e]	Santamarina et al. (1991)
Piperazine dihydrochloride	200 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish $treatment^{-1}$)	Not effective[a,e]	Santamarina et al. (1991)
Praziquantel	0, 1, 5, 10, 20 & 50 µg l^{-1}	15, 30, 60, 90, 120 min, 4 h & 16 h. 20°C. Lab study	*G. aculeati*	*Gasterosteus aculeatus* (10 fish $treatment^{-1}$)	Decrease in parasite burden[b,d]	Schmahl & Taraschewski (1987)
Praziquantel (Droncit®)	10 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish $treatment^{-1}$)	98% effective[a,e]	Santamarina et al. (1991)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Pyrantel pamoate (Trilombrin®)	50 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993b)
Quinacrine HCl (Atabrine®)	25, 100 & 200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	98% effective (25 mg l^{-1}) to 100% effective (100, 200 mg l^{-1})[d,e]	Tojo et al. (1993a)
Quinaldine	0, 26, 104 & 260 mg l^{-1}	Ca. 20, 40 & 60 s. 20–22°C. Lab study	*Gyrodactylus* sp.	*Carassius auratus, Cyprinus auratus*	Effective (26 mg l^{-1}, ca. 60 s, time needed to anaesthetise fish)[b,c]	Crigel et al. (1995)
Rafoxanide (Ranide®)	50 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993b)

Appendix 1 (continued)

Compound	Dose	Application	*Gyrodactylus* spp.	Host	Efficacy	Source
Ronidazole	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	84% effective[e]	Tojo et al. (1993a)
Secnidazole	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Sodium percarbonate	10, 20, 40, 80 & 160 mg l^{-1}	18 h. Lab study	*G. derjavini* (=*G. derjavinoides*)	*Oncorhynchus mykiss*	Not effective (10, 20 mg l^{-1}) to 100% effective (80, 160 mg l^{-1})[g]	Buchmann & Kristensson (2003)
Sodium sulpha-quinoxaline	200 mg l^{-1}	3 h. 11°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993a)
Suramin (Naganol®)	200 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993b)
Tetramisole (Nemicide®)	100 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	95% effective[d,e]	Tojo et al. (1993b)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Thiabendazole (Triasox®)	10 & 100 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[a,d,e]	Tojo et al. (1992)
Thiophanate (Nermafax 20®)	200 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective[e]	Tojo et al. (1993b)
Thiophanate	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Toltrazuril	5, 10, 20, 30 & 50 µg l^{-1}	0.3, 1, 2, 3, 4 & 6 h. 20°C. Lab study	*G. arcuatus*	*Gasterosteus aculeatus* (10–15 fish $treatment^{-1}$)	Not effective (5, 10 µg l^{-1}) to effective after 2 h (50 µg l^{-1})[a,b,c]	Schmahl & Mehlhorn (1988)
	200 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective	Tojo et al. (1993a)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Trichlorfon	Up to 2 mg l^{-1}	24 h. 23°C. Lab study	*G. elegans*	*Carassius auratus* (10 fish $treatment^{-1}$)	Not effective[b,c]	Goven & Amend (1982)
	0.25 mg l^{-1}	Continuous	*Gyrodactylus* sp.			Cited in: Schmahl (1993b)
Trichlorfon (Metrifonate)	0, 10 & 50 µg l^{-1}	25, 30, 60 & 90 min. 20°C. Lab study	*G. aculeati*	*Gasterosteus aculeatus* (10 fish $treatment^{-1}$)	Not effective[g]	Schmahl & Taraschewski (1987)
Trichlorfon (Neguvon®)	200 mg l^{-1}	3 h. 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (4–10 fish $treatment^{-1}$)	98% effective[a,e]	Santamarina et al. (1991)
	40 g kg^{-1} feed	10 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Not effective[f]	Tojo & Santamarina (1998)
Triclabendazol (Fasinex®)	6.2, 12.5 & 25 mg l^{-1}	12 h (additionally, 25 mg l^{-1} for 3 h) 15°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* (5 fish $treatment^{-1}$)	Not effective (6.2 mg l^{-1} for 12 h, 25 mg l^{-1} for 3 h) to 10% effective (25 mg l^{-1} for 12 h)[a]	Tojo et al. (1992)
Triclabendazole	40 g kg^{-1} feed	10 d & 5 d oral treatment. 15°C. Lab study	*Gyrodactylus* sp.	*Oncorhynchus mykiss* (20 fish $treatment^{-1}$)	Time dependent: parasite reduction (5 d) to 100% effective (10 d)[f]	Tojo & Santamarina (1998)
Virkon S + heat	Low concentration	25, 30, 35 & 40°C. Lab study	*G. salaris*	*Oncorhynchus mykiss* fin clips	Temperature dependent: parasite survival ranges from 119.7 min (25°C) to 9 s (40°C)[g]	Anttila et al. (2007)

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Appendix 1 (continued)

Compound	Dose	Application	*Gyrodactylus* spp.	Host	Efficacy	Source
(3) Metal salts						
Aluminium	25, 50, 100 & 200 µg l^{-1}	Continuous exposure (11–15 d) until fish died/ recovered. 8°C. Lab study	*G. salaris*	*Salmo salar* (>50 parasites $host^{-1}$)	Not effective (25 µg l^{-1}) to 100% effective after 3 d (200 µg l^{-1})[b,c]	Poléo et al. (2004)
Aluminium (& acidification)	92–250 µg l^{-1} at pH 5.0, 5.2, 5.6 & 5.9	Continuous exposure (4–30 d) 12°C. Lab study	*G. salaris*	*Salmo salar* (15 fish $treatment^{-1}$)	No effect of pH, but dose-dependent effect. At pH 5.0 effect of Al was enhanced: 100% effective after 9 d[b,c]	Soleng et al. (1999)
	Al-rich & Al-poor water (pH 5.8) & control (pH 6.3)	Continuous exposure. 11–13°C. Lab study	*G. derjavini* (*G. derjavinoides*)	*Salmo trutta* (10 fish $treatment^{-1}$)	Al-rich water: 100% effective after 3 d. Al-poor water: decrease in parasites[g]	Pettersen et al. (2006)
			G. macronychus	*Phonixus phonixus* (15 fish $treatment^{-1}$)	Al-rich water: 100% effective after 8 d. Al-poor water: not effective.[g]	
Cadmium	5 µg l^{-1}	20 & 30 d. 23°C. Lab study	*G. bullatarudis*	*Poecilia reticulata*	Not effective (after 5 & 15 d in 20 d trials) to decrease in parasite burden after 30 d[d]	Carter (2003)
	5 µg l^{-1}	60 d. 23°C. Lab study	*G. turnbulli*	*Poecilia reticulata*	Not effective[d]	Carter (2003)
Copper	10, 20, 40 & 80 µg l^{-1}	Continuous exposure until fish died/ recovered. 8°C. Lab study	*G. salaris*	*Salmo salar* (>50 parasites $host^{-1}$)	Not effective	Poléo et al. (2004)
Iron	25, 50, 100 & 200 µg l^{-1}	Continuous exposure until fish died/ recovered. 8°C. Lab study	*G. salaris*	*Salmo salar* (>50 parasites $host^{-1}$)	Not effective[c]	Poléo et al. (2004)
Manganese	100, 200, 400 & 800 µg l^{-1}	Continuous exposure (11–15 d) until fish died/ recovered. 8°C. Lab study	*G. salaris*	*Salmo salar* (>50 parasites $host^{-1}$)	Not effective	Poléo et al. (2004)
Zinc	50, 100, 200 & 400 µg l^{-1}	Continuous exposure (11–15 d) until fish died/ recovered. 8°C. Lab study	*G. salaris*	*Salmo salar*	Not effective (50 µg l^{-1}) to 100% effective after 3 d (400 µg l^{-1})[c]	Poléo et al. (2004)
	8.3, 23.7, 38.1, 68.5, 129.5 & 260.3 µg l^{-1}	1 wk pre-exposure to required conc.; after infection continuous exposure until isolated fish died/ recovered (up to 29 d) 25°C. Lab study	*G. turnbulli*	*Poecilia reticulata*	Decrease in peak parasite burden, but higher infection establishment (240 µg l^{-1}). Combined effects of parasite infection & Zn exposure more detrimental to host than parasite[c]	Gheorgiu et al. (2005)
4. Salt						
Salinity	5, 7.5, 10, 15, 20 & 33‰ salinity	Continuous exposure. 1.4, 6 & 12°C. Lab study	*G. salaris*	*Salmo salar* (fins of 6 fish for 33‰ salinity; for all others, 12 fish $treatment^{-1}$)	Not effective (5.0‰) to 100% effective after a few minutes (33‰)[b,d]	Soleng & Bakke (1997)
	33‰ salinity	5, 15, 30 & 60 min. 12°C. Lab study	*G. salaris*	*Salmo salar* (15 fish $treatment^{-1}$)	Time dependent effect: no effect (5 min) to 100% effective (60 min)[b,c]	Soleng et al. (1998)
	5–20‰ NaCl	4 d. 11°C. Lab study	*G. derjavini* (=*G. derjavinoides*)	*Oncorhynchus mykiss* (21–23 fish $treatment^{-1}$)	Not effective (5–7‰) to 100% effective (10–20‰)[b,c]	Buchmann (1997)

[a]*In vitro* tests included in study; [b]Infection intensity was determined by sub-sampling methods other than screening the entire fish; [c]Causes mortality in some or all hosts; [d]Signs of host toxicity; [e,f]Infection intensity was determined 24 h post-treatment by [e]pelvic fin clips, or [f]mucus scrapings; [g]Mortality not indicated by author; [h]No primary literature available