


Transmission dynamics of ectoparasitic gyrodactylids (Platyhelminthes, Monogenea): An integrative review

Review Article

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Abstract

Parasite transmission is the ability of pathogens to move between hosts. As a key component of the interaction between hosts and parasites, it has crucial implications for the fitness of both. Here, we review the transmission dynamics of *Gyrodactylus* species, which are monogenean ectoparasites of teleost fishes and a prominent model for studies of parasite transmission. Particularly, we focus on the most studied host–parasite system within this genus: guppies, *Poecilia reticulata*, and *G. turnbulli*/*G. bullatarudis*. Through an integrative literature examination, we identify the main variables affecting *Gyrodactylus* spread between hosts, and the potential factors that enhance their transmission. Previous research indicates that Gyrodactylids spread when their current conditions are unsuitable. Transmission depends on abiotic factors like temperature, and biotic variables such as gyrodactylid biology, host heterogeneity, and their interaction. Variation in the degree of social contact between hosts and sexes might also result in distinct dynamics. Our review highlights a lack of mathematical models that could help predict the dynamics of gyrodactylids, and there is also a bias to study only a few species. Future research may usefully focus on how gyrodactylid reproductive traits and host heterogeneity promote transmission and should incorporate the feedbacks between host behaviour and parasite transmission.

Introduction

Recent and persistent challenges caused by infectious diseases like Ebola (Bonwitt *et al.*, 2018), Zika (Lambrechts *et al.*, 2010), malaria (Tang *et al.*, 2020), Chagas (Milei *et al.*, 2009) and coronavirus disease-2019 (COVID-19) (WHO, 2020) emphasize the importance of understanding transmission dynamics from evolutionary, ecological and epidemiological perspectives. Transmission to a new host is a fundamental step in the life cycle of every parasite (Lipsitch and Moxon, 1997), and has crucial effects on the population dynamics and the fitness of both parasites and hosts (McCallum *et al.*, 2017). Mathematically, transmission is the product of three components: (1) dissemination, which is the capacity to successfully leave an infected host to be translocated to another; (2) translocation or the movement of a pathogen from an infected host to an uninfected one and (3) infectivity, which is the ability to invade new hosts after contact with infected hosts, vectors or environmental reservoirs. The product of these components is not necessarily linearly related (Antolin, 2008). Therefore, transmission is one of the most challenging processes to model and to quantify (McCallum *et al.*, 2017).

Here, we review an emerging model system for transmission experiments, *Gyrodactylus* species, which are contagious and ubiquitous ectoparasites of teleost fishes (Bakke *et al.*, 2007). These monogeneans are especially suitable for revealing novel insights into the host–parasite ecology and evolution, including population dynamics and epizootiology for several reasons. First, they reproduce *in situ* on the host and are transmitted during host contact (Bakke *et al.*, 2007). Second, all life stages can transmit between hosts and therefore transmission and infection are continuous (Bakke *et al.*, 2007). Finally, gyrodactylids have a relatively high level of host preference (Bakke *et al.*, 1992; Harris *et al.*, 2004). Indeed, this genus is one of the most species-rich taxa of Monogenea, with more than 400 described species (Harris *et al.*, 2004) where more than 73% of 319 species recorded have single hosts, while 4.1% infect more than four taxa with a wide range of up to 15 different hosts (Bakke *et al.*, 1992; Harris *et al.*, 2004).

A notable feature of gyrodactylids is their reproduction: it is characterized by extreme progenesis and a combination of different reproductive models (Bakke *et al.*, 2007). The genus mainly comprises viviparous gyrodactylids that give birth to fully grown young and, a few, oviparous species that lay eggs within the environment (Bakke *et al.*, 2007). In viviparous species, worms may contain a fully grown daughter *in utero*, which in turn encloses a developing embryo, boxed inside one another (Cable and Harris, 2002). Contrary to other helminths, these ectoparasites possess features of microparasites (e.g., direct reproduction on their host) with dynamics of macroparasites where adults are limited to only a few, asexual, parthenogenetic or sexually derived offspring (Cable and Harris, 2002).

Viviparous gyrodactylids can transmit horizontally between adult hosts and move between fish during brief contacts through four main routes: (1) direct transfer during contacts between

fishes; (2) contact between fishes and detached parasites on the substrate; (3) contact between fishes and detached parasites in the water column and (4) contact between living fishes and infected dead fishes (Bikhovski, 1961; Bakke *et al.*, 1992). However, their transmission is risky: for example, only 35–39% worms of *G. turnbulli* (originally described as *G. bullatarudis*, but redescribed as *G. turnbulli* by Harris, 1986) that attempt to transfer are successful (Scott and Anderson, 1984). And in guppies, when the host is dead, only 50% of worms leave the host and spread to a new host (Harris, 1980).

Despite the great gyrodactylid diversity, only a few species have been the subject of scientific research. For instance, initial studies of taxonomy and evolution of *G. salaris* and *G. thymalli* took place because these parasites devastated salmonid and grayling populations, respectively, in the mid-1970s (Bakke *et al.*, 2007). Also, important works include those about infection dynamics of *G. turnbulli* and *G. bullatarudis* that parasite guppies (*Poecilia reticulata*) (see Scott, 1982; Scott and Anderson, 1984; Scott and Nokes, 1984; Harris, 1989; Harris and Lyles, 1992; Richards and Chubb, 1996, 1998). More recently, guppies and their gyrodactylids have been also used in studies of parasite dynamics (see Cable *et al.*, 2000), pathology and host–parasite coevolution. Experimental infections have shown that these parasites can change the behaviour (Grether *et al.*, 2004; Kolluru *et al.*, 2006; Croft *et al.*, 2011; Reynolds *et al.*, 2018; Stephenson, 2019), mate choice (Kennedy *et al.*, 1987; Houde and Torio, 1992; López, 1999) and immune responses of their hosts (Buchmann and Uldal, 1997; Buchmann and Lindenstrøm 2002 Grether *et al.*, 2004; Kolluru *et al.*, 2006; van Oosterhout *et al.*, 2003; Cable and van Oosterhout 2007a, 2007b; Konczal *et al.*, 2020a). Recently, the transmission dynamics of gyrodactylids have been given more attention (Stephenson *et al.*, 2017; Tadir *et al.*, 2016, 2018, 2019).

We synthesize this recent research to highlight the main factors driving the spread of gyrodactylids, and to suggest further likely but untested drivers of transmission. In addition, we present the advances regarding mathematical models that measure the transmission dynamics in the genus. Particularly, this integrative review emphasizes the most studied host–parasite system within the genus *Gyrodactylus*: *Poecilia reticulata* (the host) and its two most abundant parasite species, *G. turnbulli* and *G. bullatarudis* (see Mohammed *et al.*, 2020). The significance of this review arises from the necessity to understand parasite and host features resulting from the interactions and feedbacks that make transmission possible for gyrodactylids, and at the same time, we bring an overall perspective about transmission dynamics that can be applied in other host–parasite systems.

This review is divided into five sections. First, we describe our approach to searching and evaluating the literature (Fig. 1). We then discuss the abiotic and biotic factors important in driving gyrodactylid transmission in the second and third sections, respectively. We then expose the advances in measures and mathematical models of transmission in gyrodactylids. In the final section, we offer conclusions from the existing literature, new perspectives in the study of transmission dynamics of the genus *Gyrodactylus* and highlight potentially fruitful future research directions.

Literature search and selection

To identify the main transmission promoters of gyrodactylids, we searched on two databases: ISI Web of Science and Scopus. In addition, we searched on the web search engine Google Scholar to identify possible highly cited and lesser-known articles (Beel and Gipp, 2009; Martin-Martin *et al.*, 2017). The searches were conducted in Puebla, Mexico using the browser Google Chrome

at 10:00 h Mexican Central Standard Time on 30 June 2021. On Web of Science, we searched for articles using the following search string: TOPIC: (Gyrodactylus OR gyrodactylids OR monogenea AND TOPIC: transmission OR spread OR disease OR infection). Refined by CATEGORIES: parasitology OR ecology OR evolutionary biology OR behavioural sciences, OR fisheries, OR marine freshwater biology. On Scopus, the following syntax was used: TITLE-ABS-KEY ('Gyrodactylus' OR 'gyrodactylids' OR 'monogenea' AND TITLE ('transmission', 'spread' OR 'disease' OR 'infection'). Finally, the search strings used for Google Scholar were: 'Gyrodactylus' AND 'transmission'; 'Gyrodactylids AND 'transmission'; 'Monogenea AND transmission'; 'Gyrodactylus AND 'spread'; Gyrodactylids AND 'spread'; 'Monogenea AND 'spread'. For Google Scholar our criteria for search saturation were met when 10 consecutive pages of results (100 results in total) issued no new articles that met our inclusion criteria (articles that tested or proposed results about gyrodactylid transmission).

To refine the results of the searches, three eligibility criteria were used: obtained items had to be peer-reviewed papers, in English, published from 1 January 1980 to 30 June 2021. This timeframe was set because according to a primary search, the first articles that tested *Gyrodactylus* transmission were published in the 1980s (see Tables 1 and 2), just after early studies of population dynamics in the genus (see Scott and Nokes, 1984).

After the removal of duplicates, we obtained a total of 86 records; removal of those referring to secondary bibliographical sources as books, conference records and notes reduced this to a final pool of 52 articles (see PRISMA diagram in Fig. 1). A total of 35 articles were obtained from Web of Science and 12 from Scopus; the use of Google Scholar for systematic reviews and meta-analyses has been debated (Callicott and Vaughn, 2005), however, we decided to also include 5 articles from Google Scholar (Bakke *et al.*, 1992; Soleng *et al.*, 1998; Dmitrieva, 2003; Olstad *et al.*, 2006 and Winger *et al.*, 2007) because they fulfilled the requirements of our search and contributed to the topic of interest. In total, we included 52 articles in our review (Fig. 1).

We inspected the abstracts and titles of this final pool and classified them depending on their main research question. The first group consisted of studies that measured variables directly related to parasite transmission (Table 1). In the second group, we included all the studies where the authors did not measure parasite transmission *per se*, but based on their results, they suggested variables that could affect transmission (Table 2).

Abiotic factors affecting gyrodactylid transmission

The presence or absence of parasites in host populations is the result of biotic, abiotic factors and their interaction (Anderson and Sukhdeo, 2010). Although there is no consensus about which of these factors are dominant, abiotic factors have been suggested as key drivers of host physiology, parasite multiplication and transmission (Poulin, 2020). Here, we summarize our current understanding of the abiotic factors affecting when gyrodactylids leave their host, and thus promote transmission in the genus. For gyrodactylids, abiotic factors that modify their populations dynamics are broadly water temperature and chemistry, so it is not surprising that these factors are related to their successful transmission; additionally, water flow and darkness seem to affect *Gyrodactylus* ability to spread (Soleng and Bakke, 1998; Soleng *et al.*, 1999, 2005; Poleo *et al.*, 2004).

Temperature might influence gyrodactylid spread because threshold temperatures increase components of their fitness. For instance, *G. bullatarudis* has the longest lifespan at 21°C, the highest average fecundity, and an intrinsic maximum rate of parasite

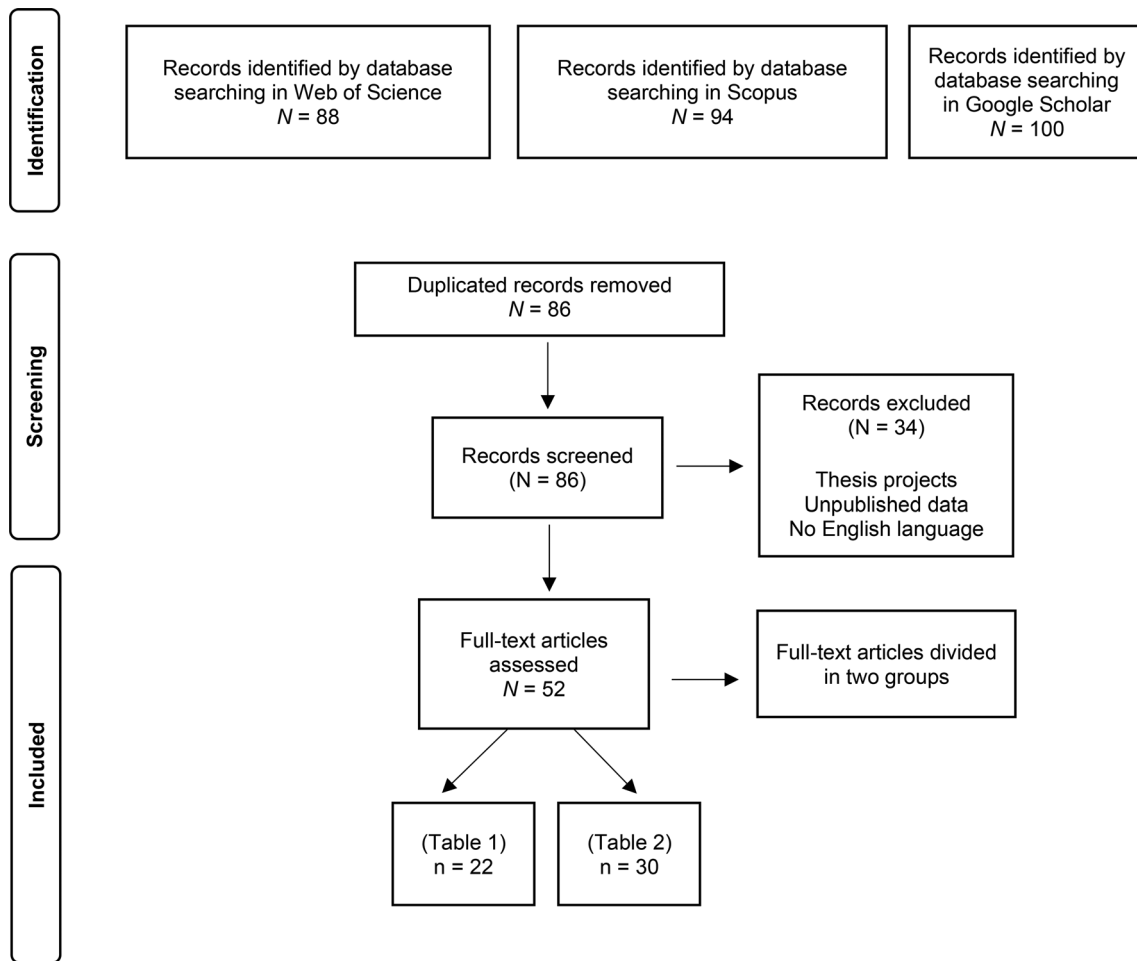


Fig. 1. Integrative review on main variables affecting *Gyrodactylus* spread on teleost fish, and the potential factors that enhance transmission. We used PRISMA guidelines (see Moher *et al.*, 2015).

population at 25.5°C, but they are not able to survive at 30°C. Within the temperature range of 6–13°C, *G. salaris* produces the maximal and higher number of offspring than other *Gyrodactylus* species (Jansen and Bakke, 1991), but at 40°C the parasite dies (Koski *et al.*, 2015). The effect of temperature on transmission has only been tested in *G. salaris*, where low temperatures reduce the rate of transmission (Bakke *et al.*, 1990), whereas high temperatures lead to a higher degree of accidental dislodgement (Harris, 1980); *G. salaris* tend to be transmissible from salmon, *S. salar* to the eel, *Anguilla Anguilla*, and vice versa at 4 and 13°C, and between host to host, *S. salar* at 1.2 to 12.2°C (Soleng *et al.*, 1998).

Higher temperatures also tend to increase host activity levels, potentially contact between hosts, and thus perhaps the likelihood of transmission (Scott and Nokes, 1984). So far, there are only indirect reports in *G. salaris* which indicate that during spring and summer in Norway, infections by these worms on *S. salar* increase, but in winter, when water temperature in Norwegian rivers are close to 0°C and fish activity is reduced to a minimum, parasite populations decline (Jansen and Bakke, 1991). Also, early studies suggested that high activity of guppies promotes the transmission of *G. bullatarudis* (Scott and Nokes, 1984), but there are no empirical studies.

Specific levels of salinity also improve gyrodactylid spread in *G. salaris*. These worms successfully transmit from salmon smolt to parr at 0.0, 7.5, 10.0 and 20.0 ‰ salinity (Soleng *et al.*, 1998) and most worms are transmitted at 7.5‰ salinity from infected salmon smolts to uninfected salmon parr (Soleng *et al.*, 1998). Although these worms are not a euryhaline species (i.e.,

organisms that can adapt to a wide range of salinities), *G. salaris* are also able to reproduce in fresh water after direct transfer from high salinities, which indicates that *G. salaris* can be dispersed through estuaries, survive in saline waters, and reproduce in fresh water (Soleng *et al.*, 1998). The effect of salinity on parasite transmission has only been studied in *G. salaris*, so it is imperative to broaden the species tested to fully understand the effect of this and other abiotic factors on the transmission dynamics of gyrodactylids.

Water flow regime is further likely important. Shoals of *P. reticulata* exposed to interrupted flow exhibited greater mean transmission rates of *G. turnbulli* compared to continuous and non-flow conditions (Reynolds *et al.*, 2019). In this experiment, a 12 h flow: 12 h no flow comprised the interrupted flow regime, and during flow, guppies aggregated in a refuge wherein flow was minimal (Reynolds *et al.*, 2019). Therefore, in interrupted flow conditions there was a higher likelihood of more direct contacts between hosts, and perhaps because guppies appear unable to discriminate olfactory cues between infected and uninfected conspecifics in these flow regimes, they were unable to avoid the elevated transmission risk (Reynolds *et al.*, 2019). This aggregation behaviour occurs in natural habitats with high predation regimes during the night (Seghers, 1974; Croft *et al.*, 2003).

Despite the lack of empirical studies, darkness itself might enhance worm activity level, resulting in transmission (Brooker *et al.*, 2011). Transmission during darkness may also minimize the chances of gyrodactylids being eaten by hosts that forage during the day (Brooker *et al.*, 2011). Further, in systems like guppies, transmission may occur when infected fish are moving between

Table 1. Studies that measured variables related to parasite transmission in the genus *Gyrodactylus*

General topic	Factors affecting transmission	<i>Gyrodactylus</i> species	Host species	References
Transmission dynamics	Abiotic Temperature	<i>Gyrodactylus salaris</i>	<i>Anguilla anguilla</i>	Bakke et al. (1990)
Transmission dynamics	Abiotic Temperature	<i>Gyrodactylus salaris</i>	<i>Salmo salar</i>	Soleng et al. (1999)
Transmission dynamics	Abiotic Temperature Salinity	<i>Gyrodactylus salaris</i>	<i>Salmo salar</i>	Soleng et al. (1998)
Transmission dynamics	Abiotic Water flow regime	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	Reynolds et al. (2019)
Transmission dynamics	Biotic Gyrodactylid routes transmission	<i>Gyrodactylus salaris</i>	<i>Salmo salar</i>	Bakke et al. (1992)
Transmission dynamics	Biotic Gyrodactylid behaviour	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	Cable et al. (2002)
Transmission dynamics	Biotic Gyrodactylid mitochondrial diversity	<i>Gyrodactylus arcuatus</i>	<i>Gasterosteus aculeatus</i>	Lumme and Zięta (2018)
Transmission dynamics	Biotic Worm maturation	<i>Gyrodactylus sphinx</i>	<i>Blennius sphinx</i>	Dmitrieva (2003)
Transmission dynamics	Biotic Worm maturation	<i>Gyrodactylus salaris</i>	<i>Salmo salar</i>	Olstad et al. (2006)
Transmission dynamics	Biotic Worm maturation	<i>Gyrodactylus gasterostei</i>	<i>Gasterosteus aculeatus</i>	Grano-Maldonado et al. (2018)
Transmission dynamics	Biotic Paratenic host	<i>Gyrodactylus bullatarudis</i>	<i>Rivulus hartii</i>	Cable et al. (2013)
Transmission dynamics	Biotic Host heterogeneity	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	Stephenson et al. (2017) Reynolds et al. (2018) Stephenson (2019)
Transmission dynamics	Biotic Body host condition	<i>Gyrodactylus kobayashii</i>	<i>Carassius auratus</i>	Zhou et al. (2017)
Transmission dynamics	Biotic Host behaviour	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	Richards et al. (2010) Johnson et al. (2011)
Parasite population dynamics	Abiotic Temperature	<i>Gyrodactylus salaris</i>	<i>Salmo salar</i>	Hendrichsen et al. (2015)
Host-parasite interactions	Biotic Host behaviour	<i>Gyrodactylus</i> spp	<i>Poecilia reticulata</i>	Croft et al. (2011)
Host-parasite interactions	Biotic Host behaviour	<i>Gyrodactylus</i> spp	<i>Gasterosteus aculeatus</i>	Rahn et al. (2015)
Host-parasite interactions	Abiotic Host sexual behaviour	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i> (Green Cobra variety)	Richards et al. (2012)
Mathematical framework of parasite population dynamics	Biotic Abiotic	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	Scott and Anderson (1984) Tadiri et al. (2019)

resting conspecifics attempting to offload their parasite burdens (Reynolds et al., 2019). Still, so far, the effect of light conditions on worm activity has been tested only in *G. gasterostei* and *G. arcuatus* (Brooker et al., 2011).

As our review illustrates, so far, the effect of only a handful of abiotic factors such as temperature, salinity, and water flow has been studied on *Gyrodactylus* transmission. Among these factors, temperature appears to be of particular importance, and more research on this factor could be particularly useful. For instance, it is known that different temperature regimes change the size of gyrodactylid haptor hooks and bars (Bakke et al., 2007) which are the organs that allow the attachment to the hosts. Temperature may have negative effects on gyrodactylids because host immunity is enhanced at higher temperatures, as reaction rates of complex proteins such as the complement cascade increase (Bakke et al., 2007). In addition, we propose studies in

water pH. Studies indicated that parasites *G. arcuatus* are locally adapted to the water in their own lake (North Uist in the Scottish Western Isles) and interestingly, virulence is related to lake pH which suggests that the evolution of virulence can be substantially affected by the abiotic environment (Mahmud et al., 2017).

Biotic factors affecting gyrodactylid transmission

Gyrodactylid features

All gyrodactylid life stages can be transmitted, but there seems to be a higher probability of transmission when worms are mature. This occurs in two situations: the worm has given birth at least once, as in *G. salaris* (Olstad et al., 2006), or when the male reproductive organ is developed, as in *G. sphinx* (Dmitrieva, 2003) and *G. gasterostei* (Grano-Maldonado et al.,

Table 2. Studies that suggest variables that could affect *Gyrodactylus* transmission based on their results or their conclusions

General topic	Factors could affect transmission	<i>Gyrodactylus</i> species	Host species	References
Parasite population dynamics	Abiotic Temperature	<i>Gyrodactylus salaris</i>	<i>Salmo salar</i>	Jansen and Bakke (1991)
Parasite population dynamics	Abiotic Temperature	<i>Gyrodactylus bullatarudis</i>	<i>Poecilia reticulata</i>	Scott and Nokes (1984)
Parasite population dynamics	Abiotic Temperature	<i>Gyrodactylus callariatis</i>	<i>Gadus morhua</i>	Appleby (1996)
Parasite population dynamics	Abiotic Water flow regime	<i>Gyrodactylus derjavini</i>	<i>Salmo trutta</i> <i>Salmo salar</i>	Mo (1997)
Parasite population dynamics	Abiotic Water flow regime	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	Hockley <i>et al.</i> (2014)
Parasite population dynamics	Biotic Heterogeneity	<i>Gyrodactylus salaris</i>	<i>Salmo salar</i>	Mo (1992)
Parasite population dynamics	Biotic Host body condition	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	van Oosterhout <i>et al.</i> (2008) Tadiri <i>et al.</i> (2013)
Parasite behaviour	Abiotic Darkness	<i>Gyrodactylus gasterostei</i> <i>Gyrodactylus arcuatus</i>	<i>Gasterosteus aculeatus</i>	Brooker <i>et al.</i> (2011)
Parasite virulence	Abiotic pH	<i>Gyrodactylus arcuatus</i>	<i>Gasterosteus aculeatus</i>	Mahmud <i>et al.</i> (2017)
Parasite fitness	Biotic Hybridization	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	Schelkle <i>et al.</i> (2012)
Transmission dynamics	Abiotic Mechanical transmission	<i>Gyrodactylus salaris</i>	<i>Salmo salar</i>	Peeler <i>et al.</i> (2004)
Transmission dynamics	Biotic Paratenic host	<i>Gyrodactylus salaris</i>	<i>Phoxinus phoxinus</i>	Bakke and Sharp (1990)
Transmission dynamics	Biotic Paratenic host	<i>Gyrodactylus salaris</i>	<i>Lampetra planeri</i> <i>Perca fluviatilis</i>	Bakke <i>et al.</i> (1990)
Transmission dynamics	Biotic Paratenic host	<i>Gyrodactylus salaris</i>	<i>Gasterosteus aculeatus</i> <i>Platichthys flesus</i> <i>Pungitius pungitius</i>	Soleng and Bakke (1998)
Transmission dynamics	Biotic Paratenic host	<i>Gyrodactylus bullatarudis</i>	<i>Gasterosteus aculeatus</i> <i>Poecilia picta</i> Other poeciliids	King <i>et al.</i> (2009)
Transmission dynamics	Biotic Paratenic host	<i>Gyrodactylus turnbulli</i>	<i>Poecilia sphenops</i> <i>Xiphophorus helleri</i> Other poeciliids	King and Cable (2007)
Species translocation	Biotic Paratenic host	<i>Gyrodactylus cichlidarum</i>	<i>Oreochromis niloticus</i> <i>Paraneetroplus</i> <i>Nebuliferus</i> Native cichlid fishes	García-Vázquez <i>et al.</i> (2021)
Host–parasite interactions	Biotic Host sexual behaviour	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	Harris (1988) López (1999)
Host–parasite interactions	Biotic Host social behaviour	<i>Gyrodactylus turnbulli</i> <i>Gyrodactylus bullatarudis</i>	<i>Poecilia reticulata</i>	Martin and Johnsen (2007) Kolluru <i>et al.</i> (2009) Stephenson <i>et al.</i> (2016) Stephenson and Reynolds (2016)
Host–parasite interactions	Biotic Host ecology	<i>Gyrodactylus stellatus</i>	<i>Parophrys vetulus</i>	Kamiso and Olson (1986)
Host–parasite interactions	Biotic Host ecology	<i>Gyrodactylus macrochiri</i>	<i>Lepomis macrochirus</i>	Hoffman and Putz (1964)
Host–parasite interactions	Biotic Host ecology	<i>Gyrodactylus turnbulli</i>	<i>Poecilia reticulata</i>	Martin and Johnsen (2007) Gotanda <i>et al.</i> (2013) Stephenson <i>et al.</i> (2015)

2018). The male reproductive system in gyrodactylids consists of a posterior testis, an anterior seminal vesicle, and a penis which becomes functional once the second embryo has commenced development (Cable and Harris, 2002). It is therefore

likely that this apparent migration of mature parasites between hosts promotes the sexual reproduction of gyrodactylids, which might maintain the genetic diversity in the population (Janecka *et al.*, 2021).

Sexual reproduction also enables hybridization, which may enhance transmission at micro and macroevolutionary scales. In terms of microevolution, there is only one experimental work that demonstrates that outcrossing between monogeneans results in a higher parasite burden over time, and an increased maximum parasite burden (Schelkle *et al.*, 2012). Hybrid genotypes appear more tolerant and resistant to the fish immune response, allowing them to maintain a reproducing population on the host for longer than parental parasites (Schelkle *et al.*, 2012). At macroevolutionary scales, new genome analysis demonstrates the role of hybridization in the evolutionary success of *G. bullatarudis* in Tobago (Konczal *et al.*, 2020a, 2020b). Indeed, there is phylogenetic evidence that co-infecting *Gyrodactylus* species may hybridize before and after host switches (Ziętara and Lumme, 2002; Kuusela *et al.*, 2007). In other parasites, hybridization may increase pathogen fecundity, infectivity, virulence, and transmission rates (Arnold, 2004; Detwiler and Criscione, 2010). However, the effect of hybridization on transmission abilities of gyrodactylids has not yet been tested. Directly comparing the transmission success of inbred and outbred strains within species, and hybrids between different *Gyrodactylus* species, represents an exciting and experimentally tractable research direction.

Despite their direct life cycle, some gyrodactylid species appear to use paratenic hosts to promote their transmission and survival under certain conditions. Paratenic hosts are optional hosts involved in the life cycle of parasites, but they are not required for its completion (Marcogliese, 1995). For instance, when experimental infections took place, *G. bullatarudis* transmit from guppies (its host) to a guppy predator killifish *Rivulus hartii*, and vice versa (Cable *et al.*, 2013). Interestingly, *G. bullatarudis* survived longer than *G. turnbulli* on *R. hartii* out of water, which suggests that the parasite is more likely to survive in the wild when *R. hartii* migrate overland between isolated guppy populations (Reznick, 1995).

Intimately related to paratenic hosts is host switching, which is the ability of parasites to use new host species (Huysse *et al.*, 2003; Araujo *et al.*, 2015). This appears to have been predominant mode of radiation within *Gyrodactylus* (Ziętara and Lumme, 2002; Meinilä *et al.*, 2004). This is clearly demonstrated by molecular evidence and phylogenetic analysis (Cable *et al.*, 1999) in groups like ‘wagneri’ which, probably evolved in two ways: (1) dissemination of euryhaline species via anadromous fishes in periglacial environments of Northern Europe, and (2) dissemination of stenohaline cyprinids through Europe during the last glaciation (Bakke *et al.*, 2002). In the first case, gyrodactylids may have switched from basal host *Phoxinus phoxinus* (ciprinidae family) to salmonids and gasterosteids, whereas in the second scenario, other gyrodactylids may have switched from the same basal host to cottids (Cottidae family) (Ziętara and Lumme, 2002).

Host switching may occur in *G. salaris*, *G. bullatarudis* and *G. turnbulli* Boeger *et al.*, 2005. The first gyrodactylid species, described originally from Baltic Salmon, has become widespread around the world infecting new fishes in the wild and in fish farms (Johnsen and Jensen, 1986, 1992). Furthermore, during experimental infections *G. salaris* can transmit to co-occurring non-salmonid hosts, like lampreys (*Lampetra planeri*), perch (*Perca fluviatilis*) (see Bakke *et al.*, 1990), minnows (*P. phoxinus*) (see Bakke and Sharp, 1990), roach (*Rutilus rutilus*), and flounder (*Platichthys flesus*) (see Soleng and Bakke, 1998) with infections that lasted a few days but without worm reproduction (Bakke and Sharp, 1990; Bakke *et al.*, 1991). Gyrodactylids that parasitize guppies can infect a range of different poeciliids and gasteroids under laboratory conditions. For example, *G. turnbulli* appeared to prefer *Poecilia sphenops* and *Xiphophorus helleri* in terms of attachment time showing longer duration of infection and higher parasite loads in comparison to other poeciliids species (King and

Cable, 2007), while *G. bullatarudis* is able to transmit and reproduce on *G. acualeatus* and *P. picta* (a sister species of *P. reticulata*; see King *et al.*, 2009). It is unclear to what extent these host ranges take place in the wild. In fact, studies found that mixed groups of *P. reticulata* and *P. picta* from Trinidad had a lower abundance of *Gyrodactylus* and were less likely to be infected than conspecifics in single-species groups (Darget *et al.*, 2013).

New evidence indicates that translocation of fishes due to aquaculture, like carp, tilapia and trout, has resulted in the co-introduction of their gyrodactylid species (García-Vásquez *et al.*, 2021) which may promote switching to native fishes. This is the case of various cichlids from three genera; *Coptodon*, *Sarotherodon* and *Oreochromis* (referred to generically as ‘tilapia’) and their *Gyrodactylus* pathogens like *G. cichlidarum* which was initially described from *Sarotherodon galilaeus*, but later was recorded in several farmed and wild cichlids on all continents except Antarctica (García-Vásquez *et al.*, 2010; Soler-Jiménez *et al.*, 2017; Zhang *et al.*, 2019). For example, at least three African gyrodactylids translocate into Mexico with their ‘tilapia’. Today, these worms are widely distributed throughout the country infecting farmed and feral ‘tilapias’ but also native poeciliids fishes (García-Vásquez *et al.*, 2021).

In summary, the gyrodactylid features that seem to promote transmission are worm maturation, hybridization, paratenic host usage and host switching. These could consist of opportunistic strategies that some *Gyrodactylus* spp. employ when environmental conditions are unsuitable for the transmission to their main hosts. Particularly, hybridization and host switching have provided positive effects at macroevolutionary scales enabling them to successfully colonize their main host but also distantly related fishes.

Host features

Heterogeneity, the individual differences between hosts in their physiology and behaviour (VanderWaal and Ezenwa, 2016; White *et al.*, 2018), means that outbreaks can be explosive if key individuals become infected (Lloyd-Smith *et al.*, 2005b; White *et al.*, 2018). Physiological and behavioural features are incorporated in epidemiological models where the transmission rate β is the product of two component rates: β_c , behavioural component, is the effective contact rate between infected and uninfected individuals, and β_p , physiological component, is the infected host’s probability of transmitting an infection given that contact (Hawley *et al.*, 2011). As with other parasites, β_p and β_c may covary in gyrodactylid transmission, having important implications for disease dynamics (Stephenson *et al.*, 2018). Recently, donor heterogeneity was evaluated in guppies parasitized by *G. turnbulli*. The results revealed that three features from donors affected transmission speed, transmission load, and the fitness of transmitted parasites (Stephenson *et al.*, 2017). These are: (1) Infection load (calculated as the number of donor worms on the day of transmission) that affected transmission speed, where heavily infected donors transmitted infection more quickly, but without a linear relationship; (2) More resistant individuals (quantified using the integral of infection load over the course of infection) transmitted more parasites in comparison to those less resistant; (3) Donors exposed to naïve recipients twice during infection – experienced donors – transmitted 3.1 more parasites than inexperienced donors exposed to naïve recipients just once during infection.

Hosts can be heterogeneous in their physiological defences against parasites, which comprise two broad mechanisms: they can directly attack parasites to reduce parasite loads (resistance), or they can limit the harm caused by these loads (tolerance) (Råberg *et al.*, 2009). Both can be either innate or acquired

(Janeway *et al.*, 2001). For instance, guppies present different innate and acquired immunity against *G. turnbulli* between and within populations (Scott and Anderson, 1984; Madhavi and Anderson, 1985; Cable and van Oosterhout, 2007a; Stephenson *et al.*, 2015); in Trinidad, guppies from Lower Aripo show a superior innate response and greater resistance than fish from Upper Aripo (Cable and van Oosterhout, 2007b). Similar variation is reported in other fishes parasitized by gyrodactylids, such as the Atlantic salmon, *S. salar* (Bakke *et al.*, 1996; Buchmann *et al.*, 2005; Gilbey *et al.*, 2006; Matějusková *et al.*, 2006), three-spined stickleback, *G. aculeatus* (de Roij *et al.*, 2010; Robertson *et al.*, 2017), goldfish, *C. auratus* (Zhou *et al.*, 2018, 2021) and rainbow trout, *O. mykiss* (Lindenstrøm and Buchmann, 2000; Lindenstrøm *et al.*, 2004).

Tolerance and resistance are responses modulated by the host's immune system and ultimately could depend on host condition (Beldomenico and Begon, 2010): host condition could therefore affect host infection intensities and therefore transmission by either improving host defence, or by providing more resources for the parasite (Cornet *et al.*, 2014). Two gyrodactylid hosts show both responses results; in guppies, *P. reticulata* there is a positive relation between condition of an initial 'source' fish (a fish with high relative condition index, K_n) and major epidemic variables (i.e., parasite incidence, peak parasite load and the degree of parasite aggregation), resulting in parasites either aggregated on 'source' hosts of high condition or transferred to hosts of high condition (Tadiri *et al.*, 2013). In goldfish, *C. auratus*, there is a negative influence of initial body condition of uninfected fish on total abundance of parasites (Zhou *et al.*, 2017). Computer models propose that larger fish are individuals with higher relative condition that support heavier parasite loads because larger fish can offer more living space for parasites (van Oosterhout *et al.*, 2008), however, further research into host body condition and fish size on mapping parasite transmission is needed.

Host behaviour drives parasite transmission dynamics across host–parasite systems. Mating behaviour, for instance, is critical for sexually transmitted bacteria, protozoa and other pathogens (Thrall *et al.*, 2000; Moore, 2002; Knell and Webberley, 2004); foraging behaviour is one of the most important routes of infection for bacteria and helminths (Moore, 2002); and social behaviour affects in general the dissemination of parasites (Altizer *et al.*, 2003; Briard and Ezenwa, 2021). In social animals like guppies, even at lower densities, the contact rate among hosts is sufficiently high to allow transmission (Johnson *et al.*, 2011). Sex-specific differences in social behaviours also drive different transmission dynamics; female guppies tend to shoal more than males (Magurran and Seghers, 1994) which results in females becoming infected earlier in the epidemic with fourfold higher likelihood of becoming infected than males (Richards *et al.*, 2010; Johnson *et al.*, 2011). Conversely, male guppies are more likely to be key in intershoal parasite transmission (Stephenson *et al.*, 2016) due to their lower propensity to shoal, as they prefer to move between shoals of females searching for mating opportunities (Croft *et al.*, 2011).

While host social behaviour affects parasite spread, gyrodactylid infection affects the social behaviour of the host. As infection becomes more prevalent within a population, individuals modify their social preferences, and thus their social network position (Funk *et al.*, 2015). For example, guppies avoid gyrodactylid-infected conspecifics, despite the negative effects on their social associations, through initiating more shoal fission events and spending less time associated with the shoal (Croft *et al.*, 2011). Similarly, three-spined sticklebacks prefer to spend more time near a group of uninfected conspecifics than near a group of infected conspecifics (Rahn *et al.*, 2015). Surprisingly, young guppies imprinted with chemical cues of infected fish prefer to

associate with, rather than avoid, parasitized individuals (Stephenson and Reynolds, 2016).

Transmission of ectoparasites, including gyrodactylids, also occurs during sexual interactions because they often involve males and females in physical contact with each other. For example, the gyrodactylid *Isancistrum subulatae* transmits to the pelagic squid *Alloteuthis subulate* during agonistic behaviour or copulation (Llewellyn, 1984). For promiscuous hosts like guppies, parasite transmission has been suggested to take place during mating or sexual harassment (Harris, 1988; López, 1999). Indeed, male ornamental guppies (Green Cobra variety) are more likely to become infected and transmit *G. turnbulli* to conspecifics during the performance of courtship behaviour that is generally directed towards females (Richards *et al.*, 2012). However, nobody has evaluated how the transmission rates of gyrodactylids during host sexual interactions compares to their transmission during non-sexual social interactions.

Host behaviour and parasite infection interact bidirectionally (Ezenwa *et al.*, 2016; Hawley *et al.*, 2021), and the interaction likely depends on infection characteristics. Negative covariation between β_p and β_c , such as the most infectious hosts being the most strongly avoided, can lead to parasite extinction in host populations, whereas a positive covariation, such as the most infectious hosts having the highest contact rates, can lead to rapid epidemic spread (Hawley *et al.*, 2011). Indeed, in the absence of infection, susceptible male guppies are less social than resistant ones, and during late infection (15–17 days post-infection), the most susceptible males spent more time shoaling (Stephenson, 2019). Similarly, uninfected guppies only avoid infected conspecifics when they are at the most infectious stage of infection (Stephenson *et al.*, 2017). This indicates a negative correlation between host infectiousness (β_p) and transmission-relevant social behaviour (β_c) in male guppies, but also that feedbacks between animal behaviour and parasite infection are dynamic, and depend on host sex and susceptibility (Stephenson, 2019).

Previous research highlights two host ecology variables that may affect the transmission of gyrodactylids: habitat structure and predation pressure. Host habitat may dictate transmission route: host–host contact could be the most important for gyrodactylids of pelagic fish (Parker, 1965; Malmberg, 1970; Harris, 1982; Kamiso and Olson, 1986), but for benthic hosts, transmission by detached parasites is probably the most important route because hosts are continuously in contact with the substrate. For example, *G. macrochiri* can achieve higher infections when wire cages containing the hosts were placed in contact with the substrate rather than suspended in the water column (Hoffman and Putz, 1964). Predators can also affect transmission. For example, because guppy shoaling behaviour increases in high-predation populations (Houde, 1998), there is a higher probability of parasite transmission there, and correspondingly, observational studies report higher prevalence in these populations (Martin and Johnsen, 2007; Gotanda *et al.*, 2013; Stephenson *et al.*, 2015).

In conclusion, host physiology, host behaviour, and their interaction (i.e., host heterogeneity) could be the host driver features of gyrodactylid transmission. Altogether, these shape individuals vulnerable to infection or particularly adept at transmitting the parasite. In addition, we propose that host ecology is an unexplored feature that probably also plays an important role in disease dynamics of gyrodactylids.

Advances in the measurement of transmission in the genus *Gyrodactylus*

Measuring parasite transmission is challenging. The most important route of transmission in gyrodactylids is direct contact between infected and uninfected fish, either between live hosts

or from a dead to a live host (Scott and Anderson, 1984). Then, according to the simple transmission function $dI/dt = \beta SI/(S + I)$, where β is the transmission coefficient (Getz and Pickering, 1983; Anderson and May, 1992; Lloyd-Smith et al., 2005a, 2005b), S , the number of susceptible hosts, and I as the number of infected hosts (Smith et al., 2009; McCallum et al., 2017), the probability of transmission in the genus *Gyrodactylus* could be at a rate βSI (frequency-dependent transmission) rather than $\beta SI/N$ (density-dependent transmission) (Heggberget and Johnsen, 1982; Johnsen and Jensen, 1986, 1992; Johnson et al., 2011; Zhou et al., 2017). Still, because pathogen transmission often occurs through more than one route, each of which may have a different functional relationship with population density (Ryder et al., 2007), it is likely that *Gyrodactylus* transmission combines frequency- and density-dependent dynamics.

Transmission models using research in guppies show that the probability of an epidemic increases with the product of duration and mean intensity of infection in the primary infected fish, and that the total parasite population increases with the host population density, but density does not necessarily affect the probability of an epidemic (Johnson et al., 2011). In species like *G. kobayashii*, faster spreading epidemics are not detected in larger populations of goldfish, *Carassius auratus* at constant density, and before day 20 of the infection, epidemics occurred faster in smaller host populations (Zhou et al., 2017). In addition, total mean prevalence and total mean abundance are not affected by host population size (Zhou et al., 2017). The same dynamic is reported in *G. salaris*, which has a prevalence of almost 100% without a density threshold of their host, Atlantic salmon (Heggberget and Johnsen, 1982; Johnsen and Jensen, 1986, 1992). In other words, gyrodactylids could persist despite low host population density (Ryder et al., 2007).

In brief, taking into account the reported information about gyrodactylid transmission and basic concepts from epidemiologic theory, we propose that if there is an efficient contact rate among individuals (i.e., effective transmission rate), frequency-dependent transmission could be prominent throughout the entire infection (Ryder et al., 2007). However, since the contact rate among individuals is not constant through the infection and host population, density-dependent transmission might take place with the drop of infection, because parasites need the largest number of susceptible hosts for arising new effective contacts (Frank, 1996; McCallum, 2001; Begon et al., 2002; Ryder et al., 2007).

Another important measurement of parasite transmission is transmission potential, R_0 , which has been suggested as the best metric of parasite fitness (Antolin, 2008). R_0 is the number of secondary infections arising from an initial infection in a population of susceptible hosts (Heesterbeek, 2002; Roberts, 2007) and theory predicts that a macroparasite can spread or invade when R_0 is greater than one (VanderWaal and Ezenwa, 2016). We only detected two studies that modelled transmission dynamics: one early study on *G. turnbulli* that proposed a model to estimate the rate of transmission as the number of parasites directly transferred from the donor fish proportional to the density of parasites at a specific time (Scott and Anderson, 1984); and one more recent study that modelled guppy-*Gyrodactylus* dynamics in small populations with the estimation of R_0 (Tadiri et al., 2019).

Conclusions and future directions

In summary, from our review of 52 articles published between 1980 and 2021, transmission dynamics in the genus *Gyrodactylus* are affected by both abiotic variables such as temperature, salinity and water flow, and biotic factors like gyrodactylid biology and host heterogeneity. Relationships between behavioural and physiological components may arise under an

assortment of contexts, and the effects of these interactions can be intensified by host behaviour–parasite feedback loops.

Since these monogeneans are directly transmitted between hosts, the probability of transmission depends on the frequency of contact between hosts but may also be density-dependent at some point during the infection (Ryder et al., 2007). *G. turnbulli* and *G. bullatarudis* that infect guppies are a good system to illustrate the complexity of transmission rates. On the one hand, female guppies could maintain frequency-dependent rates when engaging more contacts during shoaling behaviour, but also density-dependent rates because they are highly social with other females. Male guppies, on the other, may only drive a frequency-dependent transmission during sexual interactions since they have different contacts when they move among shoals to obtain mating opportunities.

Although gyrodactylids have a direct life cycle, worms post-1st birth and those with a functional male reproductive system are more likely to transmit (Olstad et al., 2006). Considering the high risk of failing to transmit to a new host, leaving at least one offspring on a host seems the optimal strategy for continuation of parasite population. Meanwhile, the sexual maturity of worms could promote a migratory behaviour for sexual reproduction, thereby increasing the genetic variability in the population. Experimental studies that test the relationship between worm maturity and transmission likelihood are needed.

Hybridization represents a tractable research direction in the study of gyrodactylid transmission. At a macroevolutionary scale, recent hybridization has played an important role in shaping genetic variation of *G. turnbulli* and *G. bullatarudis*, followed by clonal reproduction and recombination, respectively, in each species (Konczal et al., 2020b, 2021). However, parasite strains of hybrid origin may additionally show enhanced phenotypic features such as higher infectivity, expanded host range and increased transmission potential as it is suggested in other pathogens (Ravel et al., 2006). We propose empirical studies which compare transmission rates between inbred and outbred gyrodactylid strains. Importantly, human activity, migrations and climate change may increase the hybridization and prompt adaptation of many species. This could be the case of gyrodactylids which are commonly kept in aquaria and farm populations around the world (Trujillo-González et al., 2018; Maceda-Veiga and Cable, 2019; Paladini et al., 2021).

Importantly, some studies indicate that gyrodactylid microhabitat use in terms of competition and parasite density may drive transmission events (see Rubio-Godoy et al., 2012). Increases in parasite infrapopulations appear to result in gyrodactylids occupying sites that promote transmission (Mo, 1997; Harris, 1988), but more studies are needed.

Though the spread of worms is predicted to happen in a short time, parasites will not necessarily leave their host since there is a high risk of mortality during the translocation as well as low probability to attach to a suitable new host. Notably, some gyrodactylid species use host switching and paratenic hosts under specific conditions to complete transmission (Olstad et al., 2006). Indeed, host switching appears to be the predominant mode of radiation within the genus that allowed their survival during glaciation events. Today, species like *G. salaris*, *G. bullatarudis*, and *G. turnbulli* could persist and reproduce in some cases by using host species that inhabit the same environments as their main hosts. We consider it pertinent to study these possible gyrodactylid features in the wild. Remarkably, aquaculture among others is accelerating the translocation of *G. cichlidarum* and possible host-switching into native Mexican poeciliids (see García-Vásquez et al., 2017).

The rate of contact between hosts that allows gyrodactylid spread can co-vary with host immune responses, host behaviour and infection-induced behavioural changes. These changes are

likely non-uniform, where some individuals can infect only a few others while a small subset of hosts is responsible for most new infections. Host ability to transmit more gyrodactylids is then probably a result of superior tolerance, high body condition, highly social behaviour, strong social networks and elevated promiscuity. Importantly, host ecology like predation regime and aquatic environments may change disease dynamics. For instance, we propose that in guppies, females have high rates of transmission to other females during social interactions whereas males are infected or infect females during sexual interactions or when they move among shoals. This pattern could be different between high and low predation sites and depend on fish community structure.

Despite abiotic factors being the first tested factors in gyrodactylid dynamics, today these receive less research attention than biotic factors. We stress the need to conduct more studies of abiotic factors such as: water pH, since studies point a strong relationship between gyrodactylid virulence and water pH (Mahmud *et al.*, 2017); salinity, taking into consideration that some species like *G. salaris* shows wide salinity tolerance, and dark light conditions, which could trigger host-seeking behaviour. Collectively, these abiotic factors can potentially alter dynamics of gyrodactylid–host interactions and may determine transmission rates.

Overall, only a few species, mainly *G. salaris*, *G. gasterostei*, *G. kobayashii*, *G. turnbulli* and *G. bullatarudis*, have been used in studies of transmission, which is a bias with possible important implications because not all *Gyrodactylus* species necessarily show the same dynamics. Particularly, guppies and *G. turnbulli* is the only host–parasite system widely studied in terms of biotic features and transmission dynamics. We need research on more aspects of host heterogeneity, incorporating the feedbacks between host behaviour and parasite transmission in other host–parasite systems. Possibly because of the small amount of data and few experiments testing transmission, there is a lack of mathematical models that quantify and explain transmission patterns, which is a general pattern for most parasites, not only gyrodactylids.

Parasite transmission is a multi-faced process (Antolin, 2008). Here, we have synthesized research on an important parasite genus to identify host, parasite and environmental factors that influence gyrodactylid spread. With aquaculture pressures, climate change and human-mediated translocation, this investigation contributes to the understanding of pathogen transmission dynamics in times of especial urgency to the public and wildlife health.

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