



Small snails, high productivity? Larval output of parasites from an abundant host

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Abstract

1. How energy is transformed and distributed within ecosystems is a fundamental question in ecology. Parasites have been shown to play an essential role in these processes. In particular, the larval stages of trematodes, that is, cercariae, appear to contribute significantly to biomass and productivity in aquatic systems.
2. Overall, ecosystem-wide studies on parasite productivity remain scarce and have typically investigated systems with large hosts and high parasite infection rates. These studies may thus represent isolated cases of exceptionally high parasite contribution to ecosystem energetics, potentially overestimating the importance of parasite biomass.
3. Here, we quantified the productivity of trematode cercariae from a small but hyper-abundant snail intermediate host with only moderate trematode prevalence (i.e., proportion of infected individuals) in an entire lake ecosystem. We assessed individual larval output from snails and calculated the overall trematode productivity in the ecosystem.
4. Average output of individual trematode species ranged from 3 to 62 cercariae per snail per day and correlated negatively with individual cercarial size. Cercarial productivity was not uniformly distributed across trematode taxa, but dominated by the most common species that accounted for more than 80% of the productivity.
5. Total cercarial productivity amounted to 1.85 g m^{-2} , which falls within the ranges of previous studies from freshwater systems. Small but abundant snail populations may thus support a considerable productivity of parasites. However, total annual cercarial productivity in the study system amounted to 5.9 kg, which constituted just 1.2% of the standing stock snail biomass, suggesting that intermediate host populations are potentially underexploited by their parasites. Moreover, comparisons with previous studies revealed contrasting patterns of parasite productivity and biomass contribution across different habitats, showing that impacts of parasites on ecosystem energetics can vary widely.
6. Overall, we are still far away from having a complete picture of the dynamics of parasite productivity and biomass in many ecosystems. It therefore remains critical to quantify the contribution of parasites to the flow and distribution of energy and nutrients within and across habitats, to better understand their impacts on fundamental ecological principles, such as food-web structure and ecosystem energetics.

KEYWORDS

biomass, disease ecology, ecosystem energetics, food web, trematode

1 | INTRODUCTION

All organisms need energy to power their own activities and reproduction (Brown, Gillooly, Allen, Savage, & West, 2004). Consequently, how energy is transformed and distributed within ecosystems constitutes an essential question in ecology. Quantification of standing crop biomass and productivity (i.e., biomass change over time) gives fundamental insights into the energy flow and nutrient cycling in ecosystems, including the concepts of trophic levels and their dynamics (Lindeman, 1942; Odum, 1957).

Parasites occur in nearly every ecosystem and are centrally embedded in food webs where they play essential roles at all levels of trophic interactions (Lafferty et al., 2008; Marcogliese & Cone, 1997; Wood, 2007). They have been shown to significantly impact host energy budgets, affecting growth rate, metabolism and reproduction (Gérard & Théron, 1997; Lafferty & Kuris, 2009; Miura, Kuris, Torchin, Hechinger, & Chiba, 2005; Sorensen & Minchella, 1998). Ultimately, parasites have the potential to cause changes in host population structure (Hudson, Dobson, & Newborn, 1998; Kohler & Wiley, 1992; Lafferty & Morris, 1996). Moreover, host behaviour alterations by parasites can significantly affect predator–prey interactions (Lafferty & Morris, 1996; Moore, 2002; Mouritsen & Poulin, 2003; Poulin, 2010) and facilitate energy transfer within and across ecosystems, exemplifying the indirect impact of parasites on ecosystem energetics (Sato et al., 2011, 2012).

Yet, despite their integral roles in ecological interactions and energy flow, parasites have long been ignored or considered negligible with regard to their own biomass and productivity, mainly because they are individually small, typically orders of magnitude smaller than their hosts, and usually not directly visible in the environment (Loreau, Roy, & Tilman, 2005; Polis & Strong, 1996). However, the first ecosystem-wide quantification of parasitic biomass highlighted their considerable contribution to the energy budget of aquatic ecosystems (Kuris et al., 2008). Parasite biomass remarkably exceeded that of top predators in the habitat. Following this pioneering assessment, several studies have revealed comparable patterns in various freshwater and marine systems, showing that parasites, especially the asexually produced larval stages of trematodes (i.e., flukes), contribute significantly to the energy flow in aquatic ecosystems (Preston, Orlofske, Lambden, & Johnson, 2013; Soldánová, Selbach, & Sures, 2016; Thieltges et al., 2008). Consequently, these abundant and glycogen-rich larvae, the cercariae, typically ranging in size between 0.2 and 2 mm, constitute an important planktonic food source to a wide range of non-host predators (Johnson et al., 2010; Kaplan, Rebhal, Lafferty, & Kuris, 2009; Morley, 2012; Thieltges et al., 2013; Welsh, Liddell, Van Der Meer, & Thieltges, 2017).

Altogether, ecosystem-wide studies remain scarce and documented examples do not necessarily allow general conclusions to be

drawn regarding productivity patterns in other host–parasite systems. Existing studies on cercarial productivity are based on relatively large first intermediate snail hosts, such as *Lymnaea stagnalis*, *Helisoma trivolvis* and *Cerithidea californica*, with typically high infection prevalence (>30%) of parasites that can release thousands of larvae per infected snail (Kuris et al., 2008; Preston et al., 2013; Soldánová et al., 2016). Cercarial productivity depends on host size (i.e., resources available for parasite productivity) and infection prevalence in the snail population (i.e., the proportion of infected individuals). Recent studies may thus represent isolated cases of exceptionally high parasite productivity and contribution to ecosystem energetics, potentially overestimating the importance of parasite biomass. It remains to be tested whether these patterns of high trematode productivity hold in habitats where smaller snail species are used as hosts by local trematodes, and if they can be generalised.

In the present study, we quantified the productivity of trematode larvae from a small but hyper-abundant snail intermediate host, the New Zealand mudsnail *Potamopyrgus antipodarum*, in an ecosystem with only low to moderate trematode prevalence (<10%). This snail can achieve extremely high densities, often exceeding 10,000 m⁻² (Lagrué & Poulin, 2015, 2016), that may offset their small body size as a resource for parasitic trematodes. In order to assess the contribution of cercariae released by mudsnails to biotic productivity in this ecosystem, we quantified the total cercarial productivity per m² across all trematode species and calculated the output for the whole ecosystem. More specifically, our aims were (a) to quantify the cercarial output of all trematode species and calculate overall larval productivity in the ecosystem based on snail density, parasite prevalence, shedding rates from snail and cercarial body sizes, (b) to analyse how the productivity/biomass contribution is partitioned across the individual trematode taxa and (c) to compare the biotic productivity of this system to available data from the literature to assess the general contribution of trematode cercariae to productivity across different marine and freshwater systems. Overall, given snail density, we expected the cercarial productivity in the system to be comparable to, if not exceeding, the output estimated for larger-bodied, but less abundant snails and their trematodes in other marine and freshwater habitats.

2 | METHODS

2.1 | Study system

We quantified the productivity of trematode cercariae in Tomahawk Lagoon (New Zealand; 45°54'06.0"S, 170°33'02.2"E). The lake has a surface area of 0.96 ha with a maximum depth of 1.2 m. Recent studies in this system have quantified the entire community of free-living and parasitic metazoans and provided density and standing

stock biomass data for parasites and their hosts (Lagrué & Poulin, 2015, 2016). The small (4–5 mm shell length) mudsnail *Potamopyrgus antipodarum* is used as a first intermediate host by many trematode species (Hechinger, 2012; Winterbourn, 1973) and is highly abundant in the system, reaching local densities $>40,000 \text{ m}^{-2}$ (Lagrué & Poulin, 2015, 2016). This provides an ideal model system to assess the productivity of trematode cercariae from *P. antipodarum*, on which no information is available, and test whether high host density can make up for small host size.

2.2 | Snail collection and trematode identification

Snails (*P. antipodarum*) were collected in Tomahawk Lagoon from different microhabitats (rocks, sediment and macrophytes) between February and March 2018. Snails were transported back to the laboratory and screened for patent trematode infections. For this, snails were separated into individual wells of 24-well plates filled with one mL of filtered lake water and incubated for 48 hr at 20°C under constant light to induce shedding of trematode larvae. Cercariae were identified based on morphological features, using the keys of Winterbourn (1973), Hechinger (2012) and Presswell et al. (2014). Overall, 3,838 snails were screened to determine trematode prevalence (i.e., proportion of infected individuals) and to obtain infected snails for the quantification of parasite productivity. Only parasite species that occurred at prevalences higher than 0.1% were used; we did not obtain enough snails with rare trematodes for accurate productivity assessment and the contribution of these infrequent parasites to total productivity can be considered negligible. Infected snails were grouped according to their trematode species and kept in aquaria filled with aerated lake water and maintained at a constant temperature (20°C) under a 12 hr/12 hr light/dark photoperiod until the beginning of the emission experiments. Macrophytes (*Myriophyllum triphyllum* and *Elodea canadensis*) were also provided for food.

2.3 | Assessment of cercarial output

In order to analyse daily cercarial output for each of the six trematode species, infected snails ($n \geq 20$ per trematode species) of a similar size (4–5 mm shell length) were individually placed in well plates with filtered lake water and maintained at 20°C under a 12 hr/12 hr light/dark photoperiod. We chose 20°C as it is within the natural temperature range of small freshwater lakes in the region between December and April (personal observation). Snails were transferred to fresh well plates, and emerged cercariae were counted every 6 hr under a dissection microscope over the course of 48 hr. Mean daily cercarial output per snail was calculated for each trematode species.

2.4 | Assessment of cercarial productivity

As it is difficult to directly assess biomass of individual cercariae due to their small size and the requirement of large numbers of parasites, we estimated wet mass indirectly from their volume based on morphological measurements. For volume calculations, 10 live cercariae of

each species were photographed and measured. To slow down movement of the larvae for imaging, individual cercariae were anaesthetised with one drop of 99% EtOH added to the well plate containing the cercariae. Specimens were immediately placed between slide and coverslip without getting flattened. This approach allowed accurate measurement as body dimensions of cercariae were less affected by a short treatment of ethanol compared to fixation via mechanical pressure. Photographs of cercariae were taken with a top-mounted Olympus DP25 camera on an Olympus BX51 microscope. Measurements (body length/width, tail length/width) were taken from photographs with the software ImageJ (Abràmoff et al., 2004). Cercarial volumes were estimated using approximation to regular geometric shapes based on their species-specific morphology (ellipsoid, elliptical cone, cylinder; Supporting Information Figure S1). Finally, we converted the individual cercarial body volume into wet mass by multiplication with 1.1 g/cm^3 (Kuris et al., 2008). This method has been used previously in studies of cercarial productivity (Kuris et al., 2008; Soldánová et al., 2016; Thieltges et al., 2008). However, Llopis-Belenguer, Blasco-Costa, and Balbuena (2018) recently showed that such geometric approximation methods lead to a roughly threefold overestimation of the actual volume of trematode flatworms, due to their flattened bodies (see Supporting Information Figure S1). In order to allow comparison with previous studies and account for this, we provide both raw and corrected (one-third of raw values) volume estimates.

Based on these results (prevalence data, cercarial output and cercarial mass) and the available data on snail densities in the system (datasets of Lagrué & Poulin, 2015, 2016), we calculated cercarial productivity per m^2 , and for the whole Lagoon, for each trematode species separately and for all species combined. Since snail density, trematode prevalence and cercarial output are temperature-dependent and vary across seasons, cercarial production and emission in temperate regions peak in the warm summer months and are usually arrested during winter (e.g., Galaktionov & Dobrovolskij, 2003; Soldánová et al., 2016). We therefore calculated the trematode productivity for the 5 months (December–April, 151 days) during which water temperatures in the study system are high and enable cercarial productivity. Water depths at Tomahawk Lagoon do not exceed 1.2 m, and snails are present across the whole lake, which allowed us to assess the productivity for the whole system. Specifically, we calculated the following values: (a) *Cercarial output* ($\text{no. m}^{-2} 5 \text{ month}^{-1}$) = Daily cercarial output ($\text{no. snail}^{-1} \text{ m}^{-2} \text{ day}^{-1}$) \times number of infected snails (no. snails m^{-2}) \times number of summer days (d); (b) *Cercarial productivity* ($\text{g m}^{-2} 5 \text{ month}^{-1}$) = Cercarial output ($\text{no. m}^{-2} 5 \text{ month}^{-1}$) \times individual cercarial mass (g); and (c) *Total cercarial productivity in Tomahawk Lagoon* (kg) = Cercarial productivity ($\text{g m}^{-2} 5 \text{ month}^{-1}$) \times total surface area of Tomahawk Lagoon (m^2).

3 | RESULTS

3.1 | Trematode taxa and prevalence

A total of 3,838 *P. antipodarum* were screened for trematode infection. Overall, 9.87% of the snails were infected with one of 11

different trematode species. The six most dominant trematodes were Plagiorchioid sp. I, *Maritrema poulini*, *Apatemon* sp. I, *Telogaster opisthorchis*, Lepocreadiid sp. II and an unidentified Xiphidiocercaria sp. I (Table 1). Infections with *Coitocaecum parvum*, *Notocotylus* sp., Aporocotylid sp. II, Virgulate sp. I and Xiphidiocercaria sp. II were also found but excluded from the productivity assessment due to their low prevalence (<0.05%). Furthermore, 2% of the infected snails were found to have double infections and excluded from the analyses. Altogether, the six most dominant trematode species (Table 1) accounted for 96% of all infections in the system and allow an accurate assessment of the cercarial productivity in Tomahawk Lagoon.

3.2 | Cercarial output

Mean daily output ranged from 3 to 62 cercariae per infected snail, depending on the trematode species. Body volumes of individual cercariae ranged between $1 \times 10^{-4} \text{ mm}^3$ and $35.4 \times 10^{-4} \text{ mm}^3$ (Table 1). Across trematode species, average cercarial output was negatively correlated ($r = -0.8976$, $p = 0.0209$) with individual cercarial size (Figure 1). Based on our data on shedding rates, snail densities and infection prevalence, we calculated a total output of 1.6×10^6 cercariae in Tomahawk lagoon over the course of 5 months, with *Maritrema poulini* accounting for approximately 50% of the total number of cercariae (Figure 2a).

3.3 | Cercarial productivity

Based on the species-specific trematode prevalences, body volumes and cercarial shedding rates as well as snail densities, we calculated a total cercarial production of 1.85 g m^{-2} during the five summer months in Tomahawk lagoon. Plagiorchioid sp. I. was by far the most prevalent species in the study system (Table 1) and was the dominant contributor to cercarial productivity, accounting for over 80% of the overall productivity in the system (Figure 2b). Altogether, the combined trematode productivity of $1.85 \text{ g m}^{-2} \text{ 5 month}^{-1}$ falls within the ranges of the annual/summer trematode productivity reported from other freshwater and estuarine systems (Table 2).

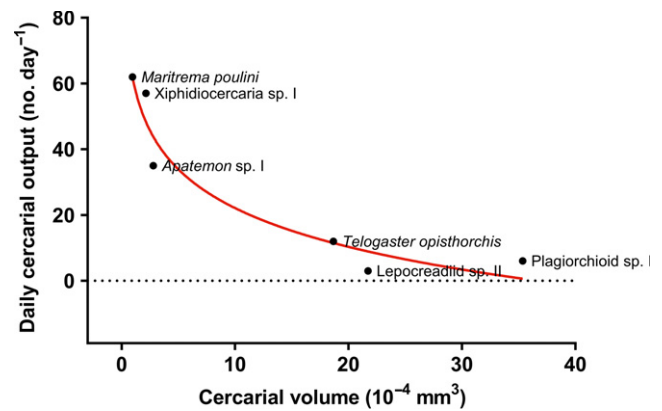


FIGURE 1 Interspecific relationship among trematodes between mean daily cercarial output (number of cercariae) per individual snail *Potamopyrgus antipodarum* and trematode-specific cercarial volume [Colour figure can be viewed at wileyonlinelibrary.com]

Taking into consideration that indirect biomass estimates based on geometric approximations for trematodes are prone to a threefold overestimation (Llopis-Belenguer et al., 2018; see Supporting Information Figure S1), we corrected the biomass by a conversion factor of 0.33, leading to a summer production of cercariae estimated at $0.62 \text{ g m}^{-2} \text{ 5 month}^{-1}$. For the whole lake (0.96 ha), this adds up to a productivity of 5.92 kg of cercariae over the 5 months of summer. Overall, cercariae represent 1.2% of the 493.2 kg of the standing biomass of *P. antipodarum* in the ecosystem (Laguer & Poulin, 2016).

4 | DISCUSSION

Our results show for the first time to what extent cercarial productivity from a small but highly abundant snail host contributes to ecosystem energetics. Despite small individual sizes and low trematode infection rates, highly dense populations of the first intermediate snail host *Potamopyrgus antipodarum* can support trematode productivity patterns comparable to those of previous studies from freshwater and marine systems. Overall, the average cercarial output (no. day^{-1}) of individual trematode species correlated negatively with individual cercarial size, supporting previous findings from marine

TABLE 1 Overview of the trematode species found in *Potamopyrgus antipodarum* from Tomahawk Lagoon showing the individual prevalence, cercarial volume and shedding rate as well as the number of infected snail per m^2

Trematode species	Prevalence (%)	Volume of single cercaria (10^{-4} mm^3)		Shedding rate ($\text{no. snail}^{-1} \text{ day}^{-1}$)	Infected snails (no. m^{-2})
		Raw	Corrected ^a		
Plagiorchioid sp. I	6.38	35.4	11.8	6	421
<i>Maritrema poulini</i>	1.22	1.0	0.3	62	81
<i>Telogaster opisthorchis</i>	0.65	18.7	6.2	12	43
<i>Apatemon</i> sp. I	0.57	2.8	0.9	35	38
Xiphidiocercaria sp. I	0.31	2.1	0.7	57	21
Lepocreadiid sp. II	0.29	21.7	7.2	3	19

^aCorrection factor of 0.33 based on an overestimation of geometric volume approximation of flatworms (Llopis-Belenguer et al., 2018).

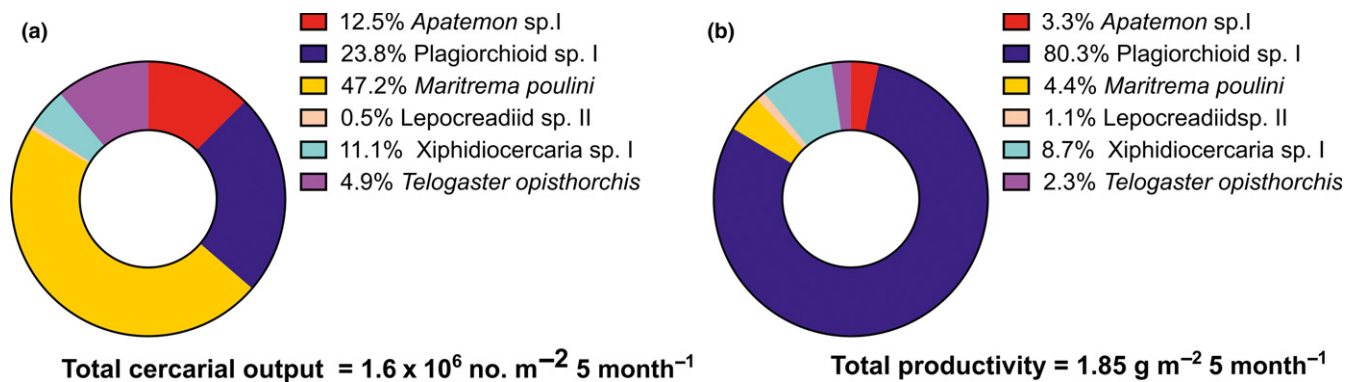


FIGURE 2 Cercarial output and productivity of the individual trematode species over 5 months of summer in Tomahawk Lagoon. (a) Output (number of emerged cercariae) per m²; (b) productivity (g) per m² [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Comparison of trematode cercariae productivity in different freshwater and estuarine systems

	Tomahawk Lagoon	Ponds in North America	Estuaries in North America
	This study	Preston et al. (2013)	Kuris et al. (2008)
Size of ecosystem (ha)	0.96	0.01–0.22	61–707
Snail host	<i>Potamopyrgus antipodarum</i>	<i>Helisoma trivolvis</i>	<i>Cerithidea californica</i>
Typical snail size (mm)	4–5 mm	8–16 mm	15–25 mm
Snail density (no. m ⁻²)	6,590	106	n/a
Trematode prevalence (%)	9.76	32–35	n/a
Trematode shedding rate (no. snail ⁻¹ day ⁻¹)	3–57	14–1,660	n/a
Trematode productivity (raw data)	1.85 (g m ⁻² 5 month ⁻¹)	0.7–2.2 (g m ⁻² year ⁻¹) ^b	0.96–4.32 (g m ⁻² year ⁻¹)
Trematode productivity (corrected ^a)	0.62 (g m ⁻² 5 month ⁻¹)	–	–

^aCorrection factor of 0.33 based on an overestimation of geometric volume approximation of flatworms (Llopis-Belenguer et al., 2018). ^bProductivity was converted to wet mass based on a wet-to-dry mass conversion factor of 0.1 (Benke, 1984; Preston et al., 2013).

and freshwater host–parasite systems (Preston et al., 2013; Thieltges et al., 2008). This pattern follows the expected theoretical relationship between offspring size and offspring number (e.g., Lloyd, 1987; Winkler & Wallin, 1987), and highlights that energy can only be allocated along a universal trade-off between individual cercarial size and cercarial numbers.

Here, *Plagiorchioid* sp. I was by far the most prevalent trematode. Although this species releases a low number of relatively large cercariae, it was the main contributor to total cercarial productivity, accounting for more than 80% of the overall productivity. A similar distribution pattern of cercarial mass has been previously reported for freshwater systems in California, where 92% of the total cercarial production was made up by one trematode species (Preston et al., 2013). These results indicate that direct parasite contribution to energy budgets of aquatic ecosystems is not partitioned equally across the individual trematode taxa, but is rather dominated by few individual species. Such patterns might have important implications for the distribution of energy in the aquatic environment as cercariae show species-specific temporal and spatial dispersal strategies, depending on their target host (Combes, Fournier, Moné, & Théron, 1994; Morley, 2012). For example, the majority of cercarial productivity in our system is concentrated in the bottom-dwelling larvae of *Plagiorchioid* sp. I. Since cercariae are important food items for

non-host predators (Johnson et al., 2010; Thieltges et al., 2013; Welsh et al., 2017), this has consequences for where and to what extent this energy is available to predators.

Overall, our results show that small snail hosts with low parasitic prevalence (<10%) can still lead to a considerable output of cercariae, due to their high abundance. This amounted to a productivity of 1.85 g m⁻² over five summer months, which falls within the ranges reported from freshwater ponds and estuarine systems in North America (Table 2). Since snail densities, trematode infection rates and cercarial output drastically decrease during winter (Lagroe & Poulin, 2015, 2016; Morley, 2012; Thieltges & Rick, 2006), the calculation of trematode productivity in the warm summer months should provide a representative estimate for the annual productivity in Tomahawk Lagoon, and our results should therefore be comparable to previous assessments from freshwater systems. Overall, the similarity of trematode productivity per m² among ecosystems is striking, considering that the properties of the first intermediate hosts determining cercarial productivity, such as host abundance and size, trematode prevalence and trematode community composition are highly different across these ecosystems.

In contrast with the similarities regarding cercarial productivity over time, standing stock biomass of parasites can be highly variable among different systems, with different life stages dominating

parasite biomass in different habitats. In North American ponds and estuarine systems, asexually multiplying juvenile stages in snail first intermediate hosts constituted most of the parasite standing stock biomass, even exceeding that of some free-living taxa in the habitats (Kuris et al., 2008; Preston et al., 2013). On the other hand, in several New Zealand lakes, including our study system, within-snail juvenile trematodes contributed relatively little to total parasite biomass; the small size of snail hosts can only accommodate a small standing stock of these life stages. In these systems, metacercariae in their second intermediate hosts were the major contributors to total standing parasite biomass. Still, they never exceeded the biomass of the major free-living groups, which were 1–2 orders of magnitude larger (Lagrué & Poulin, 2016). Remarkably, our present results show that summer production of cercariae was 7.4-fold that of the trematode standing stock biomass in Tomahawk Lagoon (0.25 g m^{-2} , Lagrué & Poulin, 2015), which is far higher than the 1.3-fold to 2.2-fold difference between annual cercarial productivity and parasite standing stock in saltmarsh systems (Kuris et al., 2008). This suggests that the relationship between standing stock biomass and productivity of trematodes can differ widely between aquatic ecosystems.

Moreover, other aquatic ecosystems such as rivers and marine systems have been shown to support varying levels of productivity and biomass of parasites. In contrast to the productive lake ecosystems mentioned previously, standing stock parasite biomass in oligotrophic streams amounted to only a fraction of free-living consumer biomass and occurred mainly in fish hosts (Paseka, 2017). In marine systems, annual cercarial productivity of trematode species ranges from 0.001 g m^{-2} to 123 g m^{-2} , indicating that trematode contribution to ecosystem energetics varies to a greater extent than in freshwater habitats (Thieltges et al., 2008). Altogether, these contrasting patterns indicate that the role of parasites in ecosystem energetics can vary extensively between aquatic habitats and will require further investigation from different systems for general conclusions.

Most previous analyses of trematode productivity have been based on body volume estimates assuming that parasites have regular geometric shapes (Kuris et al., 2008; Preston et al., 2013; Soldánová et al., 2016; Thieltges et al., 2008). However, these regular shapes (i.e., ellipsoids, cylinders and cones) do not accurately describe the flattened morphology of flukes, including their cercariae. As exemplified by adult flatworms, this indirect approach leads to a threefold overestimation of volumes, which has a severe impact on ecosystem-wide biomass extrapolations (Llopis-Belenguer et al., 2018). For this reason, we applied a correction factor of 0.33 when calculating the overall cercarial productivity for the whole lake system. Based on these corrected values, we estimated an annual cercarial productivity in Tomahawk Lagoon of 5.9 kg. Compared to the standing stock biomass of the first snail intermediate host, trematodes transform just 1.2% of this total host biomass into cercarial tissue (cf. Lagrué & Poulin, 2016). Despite the high snail abundance, overall trematode prevalence in Tomahawk Lagoon is lower than in other systems where infection rates often reach 30% or more in summer (e.g., Preston et al., 2013; Soldánová et al., 2016). This

further supports the assumption of Lagrué and Poulin (2016) that intermediate host populations in the system are potentially underexploited by parasites and that parasite populations might rather be constrained by other factors, such as transmission dynamics or other epidemiological processes than by limited host resources. Unlike in other systems, cercarial productivity in Tomahawk Lagoon is far from exceeding the total biomass of keystone free-living taxa, such as top predators (Kuris et al., 2008; Preston et al., 2013).

Parasites undoubtedly play important roles in ecosystems, including their energetics, as they use and transform their hosts' energy and, in the case of free-living larval stages, directly contribute to the redistribution of this energy in the system. Recent studies have uncovered some contrasting patterns of parasite productivity and biomass contribution across different habitats, showing that impacts of parasites on ecosystem energetics can vary widely. Since we show how small but abundant snail populations can support a considerable productivity of parasites, it would be revealing to assess the specific productivity of other small freshwater gastropods that constitute important trematode hosts, such as the widespread *Gyraulus* spp. Overall, we are still far away from having a complete picture of the dynamics and function of parasite productivity and biomass in many ecosystems, for example, we are still lacking comparable assessments from terrestrial habitats. Although parasites might account for up to 50% of all the species on Earth (Poulin, 2014), we currently lack an understanding of their role in the distribution of biomass on a global scale (Bar-On, Phillips, Milo, & Falkowski, 2018). It therefore remains critical to quantify the contribution of parasites to the flow and distribution of energy within and across habitats, to better understand their impacts on fundamental ecological principles, such as food-web structure and ecosystem energetics.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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