HIGHLIGHTED STUDENT RESEARCH

How predator and parasite size interact to determine consumption of infectious stages

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Abstract

Parasites are important players in ecological communities that can shape community structure and influence ecosystem energy flow. Yet beyond their effects on hosts, parasites can also function as an important prey resource for predators. Predators that consume infectious stages in the environment can benefit from a nutrient-rich prey item while concurrently reducing transmission to downstream hosts, highlighting the broad importance of this interaction. Less clear, however, are the specific characteristics of parasites and predators that increase the likelihood of consumption. Here, we determine what combination(s) of predator and parasite morphological traits lead to high parasite consumption. We exposed the infectious stages (cercariae) of five trematode (fluke) taxa to aquatic insect predators with varying foraging strategies and morphologies. Across the 19 predator—parasite combinations tested, damselfly predators in the family Coenagrionidae were, on average, the most effective predators of cercariae, consuming between 13 and 55% of administered cercariae. Large-bodied cercariae of *Ribeiroia ondatrae* had the highest average vulnerability to predation, with 37–48% of cercariae consumed. The interaction between predator head width and cercariae tail size strongly influenced the probability of consumption: small-bodied predators were the most effective consumers, particularly for larger tailed parasites. Thus, the likelihood of parasite consumption depended strongly on the relative size between predator and parasite. Our study helps establish that predation on free-living parasites largely follows a broader predator–prey framework. This will help to identify which predator and parasite combinations will likely have high consumptive interactions, potentially reducing parasite transmission in natural populations.

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Parasites can make up large proportions of a community's biomass and may serve as valuable prey items for numerous predators. Identifying the drivers that determine parasite consumption will allow us to understand the likelihood of parasites serving as a viable food source for various predators and how predation on parasite can potentially reduce parasite transmission. Using an experimental approach, we demonstrate that predation on parasites is largely driven by a combination of predator and parasite size, with highest consumption patterns observed with smaller predators feeding on larger parasites.

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Introduction

Parasites are influential in structuring biological communities, including the trophic interactions that mediate how energy flows through ecosystems (Hudson et al. 2006, Strauss et al. 2017, Paseka et al. 2020). Typically, parasites influence ecological communities and trophic interactions by altering host fitness or behavior (Wood and Johnson 2015; Shoemaker et al. 2019). In intertidal environments, for instance, marine snails infected with trematodes have higher grazing rates compared to uninfected snails, resulting in shifts in the intertidal macroalgae communities when parasitism is high (Wood et al. 2007). For trophically transmitted parasites that depend on predation as a vehicle for moving between host species, infection can lead to changes in the behavior, physical structure, or appearance of hosts that ultimately increase their vulnerability to predators (Mouritsen and Poulin 2003; Duffy et al. 2005; Goodman and Johnson 2011). While research into the diverse ecological

roles of parasites has grown steadily in recent decades (e.g., Lafferty et al. 2008; Preston et al. 2016Borer et al. 2020), it has largely focused on the effects of parasitism as mediated through changes in their hosts, rather than on the direct value parasites offer as nutrient resources for various consumers (Wood and Johnson 2015).

A more direct pathway through which parasites can shape energy flow and trophic interactions is as prey for other consumers (Lafferty et al. 2006; Thieltges et al. 2008). Free-living infectious stages of parasites—including fungal spores, trematode miracidia and cercariae, and nematode larvae—can provide nutrient-rich resources for many predators (e.g., Preston et al. 2013; McKee et al. 2020). Identifying and quantifying the diversity and intensity of interactions between predators and parasites has the potential to improve not only our understanding of the ecological roles of parasites, but also the compositional structure of, and energy flow through, ecosystems. For instance, in assessing the food web structure of a salt marsh community, Lafferty et al. (2006) reported that parasites were involved in 78% of food web links, such that incorporation of parasites increased estimates of food web connectance by 93%. Concurrently, predation on parasite infectious stages can also inhibit transmission to subsequent hosts (Johnson et al. 2010; Hopkins et al. 2013; Rohr et al. 2015). Predator-mediated declines in transmission have been detected across a range of host–parasite systems in both aquatic and terrestrial ecosystems, including consumption of fungal zoospores by zooplankton (Searle et al. 2013; Kagami et al. 2014), of nematode larvae by carnivorous fungi (Carvalho et al. 2009), and of digenetic trematode (flatworm) cercariae by aquatic macroinvertebrates (e.g., Schotthoefer et al. 2007; Orlofske et al. 2012).

With growing recognition of the widespread nature of predation upon free-living infectious stages, including the potential for such interactions to shape energy flow and reduce downstream transmission, there is a need to better integrate predator–parasite interactions into a broader predator–prey framework. Notably, many aquatic infectious stages should be considered as part of the free-living zooplankton community (Morley 2012), for which there is a rich history of predation research (see reviews by Lampert 2006; Seda and Petrusek 2011). This knowledge can consequently be applied to better identify what combinations of predator and parasite characteristics are likely to maximize the likelihood of infectious stages being consumed (Johnson et al. 2010; Thieltges et al. 2013). Free-living parasites and their predators should thus fit within the broader scope of predator–prey literature as these taxa can vary in trait values that have been established as key drivers in shaping consumption of zooplankton. For instance, free-living infectious stages of parasite taxa often vary dramatically in body size, which is a key trait in determining the likelihood of predation upon zooplankton (e.g., Vanni 1988; Tollrian 1995).

Studies of predator–prey interactions in freshwater ecosystems, including those between zooplankton and their invertebrate or vertebrate predators, tend to highlight the importance of prey body size (Brooks and Dobson 1965; Murtaugh 1981), prey behavior (Loose and Dawidowicz 1994), habitat use (Hays 2003), and predator size (Post et al. 2008). Prey must be large enough to be perceived by predators, while predators need to have a suitable gape size for catching and consuming potential prey items (Woodward et al. 2005). Concurrently, predation risk may be influenced by circadian activity patterns by prey, as illustrated by diel vertical migration patterns of zooplankton (Hays 2003), alongside ontogenetic shifts in diet preference and consumption ability of predators (Miller and Rudolf, 2011; Nakazawa, 2015).

Incorporating such insights derived from predation risk upon zooplankton is useful for studies investigating the consumption of parasite free-living parasite stages. In aquatic habitats, for example, infectious agents often range from microscopic fungal zoospores (~5 μm) (Berger et al. 2005) to trematode cercariae (~1500 μm, Miller 1929), to marine isopods (~9000 μm, Jay 1989), which collectively span the range of micro- and macrozooplankton. Furthermore, free-living infectious agents are known to display variation in behavior similar to that of zooplankton. This includes variation in the timing of greatest activity (Hannon et al. 2018), and a broad gradient of activity level, ranging from highly active swimming behaviors to more passive floating in the water column (Haas 1994).

Digenetic trematodes offer a valuable study system in which to investigate interactions between predators and parasites. Trematodes, which represent one of the most abundant and diverse parasite groups (Poulin and Morand 2000), depend on free-living infectious stages to move among host taxa. Within the trematode life cycle, asexual reproduction occurs in a molluscan first intermediate host, often a snail, resulting in the emergence of a vulnerable and short-lived (typically < 24 h) free-living aquatic stage called a cercaria (Esch et al. 2002). Among the roughly 25,000 species of trematodes (Esch et al. 2002), there is tremendous diversity in cercariae body size (from ~120 to 1500 μm), morphology (e.g., Koehler et al. 2012), and behavior (e.g., Haas 1994). In addition, trematodes can have substantial burdens on both human (Colley et al. 2014) and wildlife health (Johnson et al. 2003), while frequently comprising substantial biomass in aquatic habitats (e.g., Kuris et al. 2008; Preston et al. 2013; Rosenkranz et al. 2018).

Since cercariae typically fall within the size range of zooplankton (who are ~0.2–2000 μm—Hansen et al. 2000), they are vulnerable to many common aquatic planktivores (Morley 2012), including mollusks, crustaceans, freshwater insects, small fishes, and larval salamanders (e.g., Schotthoefer et al. 2007; Kaplan et al. 2009; Orlofske et al. 2012;

Welsh et al. 2014; Mironova et al. 2019). This includes predators that passively consume cercariae (e.g., filter feeders) as well as more active predators. For instance, while filter feeders such as mollusks may passively consume cercariae, nymphal dragonflies and damselflies (order Odonata) actively prey upon cercariae, reducing cercariae abundance by up to 63% in experimental trials (Orlofske et al. 2012). Furthermore, nymphal odonates vary broadly in their foraging strategy both among and within taxonomic families. Certain taxa utilize an ambush style of foraging strategy (e.g., taxa in the genus *Libellula*), while others actively move through the habitat in search of prey (Corbet 1980). Nymphal odonates also have high inter- and intraspecific variations in body size, gape size, mobility, and trophic position (Corbet 1980), facilitating an assessment into how patterns of infectious stage consumption depend on predator and parasite characteristics. Predator habitat preference and gape size can also vary throughout ontogeny, highlighting the importance of studies that quantify how intraspecific (predator developmental stage) and interspecific (predator identity) variation affect infectious stage consumption patterns. Thus far, however, there is little empirical work investigating how interactions between predators and free-living infectious stages vary in response to the size variation of both prey and potential predators, despite a strong foundation for such research based on free-living zooplankton and their planktivorous predators (Sih et al. 1985; Scharf et al. 2000).

To investigate how differences in predator and parasite traits affect their trophic interactions, we used an experimental approach to quantify how consumption of five distinct cercaria (parasite) morphotypes varied among up to five aquatic insect families (predator), with a total of 19 of 25 possible combinations examined. These five families of aquatic insect taxa, which encompassed many of the more common aquatic insects found in the system, ranged from active predators to herbivores. Similarly, the five trematode taxa captured variation in both cercariae size and swimming behavior. We expected that the likelihood of predation would be a function of both predator and parasite identity, and in particular, their morphological characteristics. Specifically, for parasites, we hypothesized that larger, more active cercariae would be consumed at higher proportions. For predators, we hypothesized that smaller taxa and earlier developmental stages would consume more cercariae due to a matching in appropriate gape size, with additional variation owing to differences in foraging strategies. Taken together, this work aims to integrate predator–parasite consumption patterns with established predator–prey literature (especially for zooplankton) to facilitate the identification of predator and parasite trait combinations that cause substantial predation upon cercariae. Assimilating parasites into a general predator–prey framework will further facilitate identification of the conditions under which parasites function as an important nutrient resource, as well as when predators are likely to inhibit parasite transmission by consuming infectious propagules.

Materials and methods

Study system

To test how variation in parasite identity and morphology alter vulnerability to predation, we used five morphotypes of common freshwater trematode cercariae from the Bay Area of California: *Australapatemon* sp. (AUSP), *Cephalogonimus americanus* (CEAM), *Echinostoma* sp. (ECSP), *Ribeiroia ondatrae* (RION), and an unidentified member of the family Spirorchiidae with a brevifurcate-apharyngeate morphotype (BREVI) (Goodchild and Kirk 1960). These cercariae morphotypes capture a broad range in both morphological and swimming behaviors (Table 1) as well as represent the majority of cercariae morphotypes that are readily available in the first intermediate host in our system (see Richgels et al. 2013). For predators, we used nymphal insects from five families commonly found within the same habitats as the focal trematodes (McDevitt-Galles and Johnson, 2018), including four odonate families: Aeshnidae (AESH) and Libellulidae (LIBE), both in the suborder Anisoptera (Dragonflies), and Coenagrionidae (COEN) and Lestidae (LEST), both in the suborder Zygoptera (Damselflies). Members of these families have been previously identified as cercariae predators (Orlofske et al. 2012) and can have high variation in morphology and foraging strategy. The damselfly family Coenagrionidae is one smaller odonate taxa found in our system, with the dragonfly family Aeshnidae being one of the largest. These taxa can utilize a combination of foraging strategies, including ambush and active foraging, with the latter being the overall dominant strategy in our system. Finally, we also performed trials with the family Baetidae (BAET) within the order Ephemeroptera as a 'positive control', which were not expected to eat cercariae as they consume detritus and periphyton (Jacobus et al. 2019).

We collected trematode parasites and aquatic insect nymphs from ponds in the San Francisco Bay Area of California between May and August of 2019. To obtain trematode cercariae, we placed infected snails (*Helisoma trivolvis*) individually in 50 mL centrifuge tubes with dechlorinated, UV-sterilized, and carbon-filtered freshwater (hereafter referred to as 'treated water') and monitored them for cercariae emergence over 24 h following a natural light:dark cycle. Cercariae were identified using morphological features (Schell 1985). Infected snails were housed in treated water at 22 °C and fed a mixture of Tetramin™ (fish food), agar and calcium. Upon collection, all predators were

Table 1 Trait values of the predators (aquatic insects) and trematode parasite cercariae used in this study

Taxa	Morphological traits		Life history traits	Source
Predator	Body size (mm) $\pm$ 1 sd	Head width (mm) $\pm$ 1 sd	Trophic level	
Aeshnidae	17.10 ± 9.81	4.68 ± 2.00	Predator	Corbet (1999)
Libellulidae	12.00 ± 4.58	3.74 ± 1.19	Predator	Corbet (1999)
Coenagrionidae	10.90 ± 3.28	2.78 ± 0.49	Predator	Corbet (1999)
Lestidae	18.20 ± 4.68	3.73 ± 0.52	Predator	Corbet (1999)
Baetidae	6.70 ± 1.22	1.22 ± 0.21	Grazer	Jacobus et al. (2019)

Parasites	Body Size (µm)	Tail Size (µm)	Total Size (µm)	Peak shedding	Swimming behavior	2nd intermediate host	Source
Ribeiroia ondatrae	427	651	1078	Nocturnal	Continuous	Amphibian/fish	Orlofske et al. (2015), Schell (1985)
Echinostoma sp.	344	428	722	Diurnal	Continuous	Amphibian, fish, snails	Orlofske et al. (2015), Schell (1985)
Brevifurcate-apharyngeate	203	605	808	Diurnal	Continuous	None	Goodchild and Kirk (1960)
Australapatemon sp.	134	140	273	Diurnal	Intermittent	Leech	Orlofske et al. (2015), Calhoun et al. (2020)
Cephalogonimus americanus	374	158	533	Diurnal	Intermittent	Amphibian	Orlofske et al. (2015), Schell (1985)

Predator morphological traits were directly measured from the specimens in the experiment, with values representing mean $\pm$ 1 sd. Predator foraging information was collected from published literature. For parasites, both morphological and behavioral traits were collected from published literature

identified to family and housed in treated water. Odonata nymphs were fed 1–3× per week using a mixture of *Daphnia* and ostracods.

Predation trials

Twenty-four hours before feeding trials, infected snails were placed in 50 mL centrifuge tubes with treated water. At the peak emergence time for each parasite (Hannon et al. 2018), cercariae from multiple snails (between 2 and 12 individuals) were pooled, and 30 cercariae of the appropriate parasite were added to containers (dimensions: 79.4 mm × 77.8 mm × 52.4 mm) housing an individual predator in 60 mL of treated water. Cercariae were no older than 5 h, ensuring they were active during the experimental period. To confirm our ability to detect "leftover" cercariae, we included a minimum of 20 control trials that received cercariae but no predators for each parasite-by-predator combination. Trials using all five predator families were conducted for *Australapatemon* sp., the Brevifurcate-apharyngeate cercaria, and *Echinostoma* sp.; due to limitations in predator

availability, only two predators (LIBE and COEN) were used with *C. americanus* and *R. ondatrae*. In total we conducted 558 individual predator—parasite trials, including predator-free controls. Excluding control trials, we had an average of 18 replicates for each predator–parasite combination (minimum of 10 and maximum of 20) (Supplementary Material Table 1).

After administering cercariae to containers, we initiated trials by adding appropriate predators. Predators were fasted for 24 h prior to the start of each assay following previously established protocols (Orlofske et al. 2012). The lighting of the experimental room was kept consistent with natural lighting at the time of peak cercarial emergence (i.e., light if peak emergence was during diurnal periods, and dark if peak emergence was during nocturnal periods). All trials were run for 1 h following established timeframes from previous experiments (Orlofske et al. 2015; Welsh et al. 2019), after which predators were removed and remaining cercariae were counted under a SZX10 Olympus dissecting microscope. We assumed that missing cercariae were consumed by predators or removed though alternative pathways, such

as passive filtration through the insect's branchial baskets. Each predator was used only once, after which it was preserved in 95% ethanol and measured (head width and body length). While most remaining (i.e., leftover) cercariae were counted within 24 h of trial completion; we counted *Australapatemon* sp. cercariae after the addition of four drops of gram stain iodine (Azer Scientific, item #ES803E) to help visualize this smaller taxon.

Predator and parasite traits

For parasites, we focused on morphological traits hypothesized to affect consumption, including body, tail, and total length (all in μm). Values for all morphological traits were obtained through published studies (see Table 1). Although there is likely within-taxon variation for these values, there is much larger variation in size across the different morphotypes than within-taxon. As a key goal of this study is to assess broad taxon-level variation in consumption patterns, we are more interested in across-taxa differences than the more subtle within-taxon variation. For the set of cercariae considered here, swimming behavior correlated with morphology, such that larger morphotypes tended to be more vigorous and continuous swimmers (see Supplementary Material Fig. 1).

For predators, we considered total body length (mm) and head width (mm); due to correlations between these characteristics (Pearson correlation coefficient = 0.82, Supplementary Material Fig. 2 and Supplementary Material Fig. 3), we focused on head width as it better corresponds to gape size (Catania et al. 2016)—a key morphological trait of interest in this study (Wilson 1975; Ovadia and Schmitz 2002). To disentangle the effect of variation in size *among* predator taxa from variation in size *within* predator taxa, we used two Z-score metrics for head width: a scaled metric across all predators (for which a value of 0 represented the mean head size across all predator taxa), and a scaled metric across the different families (for which a value of 0 represented the mean head size for a specific predator family across all replicates). Furthermore, as all the predators used in our experiment are juvenile insects with determinate growth, scaled predator taxa head width within a given family serves as a proxy for variation in taxon developmental stage. Where smaller values of family level predator taxa head width represent earlier developmental stages, larger values represent later developmental stages. While the family level predator head width does not account for variation in size at the genus and species level, we expect that the family size variation should strongly capture the variation at the lower taxonomic level. Based on previous work with the Odonata taxa at our field sites, we know there are limited number of genera found in each of the four odonate families, with only two dominant genera identified in the families Coenagrionidae,

Lestidae and Aeshnidae and six genera identified in Libellulidae (McDevitt-Galles and Johnson 2018). Furthermore, these different genera were observed to have similar size ranges within the genus and family levels (see McDevitt-Galles et al. 2018). We do, however, acknowledge that variation among specific predator species could significantly influence the observed consumption patterns.

Statistical analysis

We assessed: (i) how consumption by predators and vulnerability of cercariae varied among taxa and in response to specific morphological sizes; (ii) the consistency in consumption probability for each parasite-predator combination across predator developmental periods (i.e., family level scaled head width); and (iii) how interactions between predator and parasite morphological traits shaped the amount of consumption (total number of cercariae 'lost' relative to number administered). For all statistical analyses, we used generalized linear mixed effects models with a binomial distribution and a logit link function using the lme4 package (Bates et al. 2014) in the R statistical environment (R Core Team 2019).

(i) Variation in parasite consumption among taxa and their associated traits

To quantify variation in consumption across predator and parasite taxa, we built a random intercept-only model with random intercepts for predator and parasite identity. This variance partitioning analysis addressed the relative amount of variance associated with predator identity as opposed to parasite identity (Gelman and Hill 2007). To assess how consumption varied among predator types, we built mixed effects models for each parasite species/morphotype, with predator identity as the only fixed effect and a random effect for the site (i.e., pond) from which the predator was obtained to account for environmental effects. We used Tukey's pairwise comparisons to evaluate differences in consumption ability across predator taxa and control groups using the glht function in the multcomp package (Hothorn et al. 2013).

To assess how predator and parasite morphological traits *jointly* altered consumption, we removed both the cercariae-only control groups and the Ephemeroptera trials as we did not observe Ephemeroptera to be active consumers of cercariae due to their herbivorous diet (Jacobus et al. 2019). We then used the mixed effect modeling framework to test how parasite length (total-, body-, and tail length in separate models), and the interaction between the predator's scaled head width and the predator's family level scaled head size, affected cercariae consumption. By including the interaction between the predator's head with and the taxa's scaled family level head width, we can independently assess how both *overall* head

size variation *across* all the predators and the *relative* head size variation *within* a given predator taxa's family shaped consumption patterns. We included random intercept terms for parasite and predator identity to account for additional variation in consumption. After building this full model, we removed individual terms to assess the significance of each term using likelihood-ratio tests between full and reduced models (Bolker 2008).

(ii) Consistency of consumption patterns across developmental stages

To assess the consistency of predator–parasite interactions across predator development (ontogeny), we modeled the probability of cercariae consumption as a function of a three-way interaction among parasite taxa, predator taxa, and the scaled family level predator taxa head width, including all two-way interactions. We used odonate taxa's family level head width as a proxy for predator development stage. By evaluating the predicted slopes for the effect of family level scaled head width variation on consumption for each parasite–predator combination, we aimed to assess which interactions were consistent across predator development (i.e., limited effect of head width on consumption), and which were highly varied (i.e., larger effects of head width on consumption). After building the full model, we removed terms, reran the model, and compared models and using likelihood-ratio tests (Bolker 2008).

(iii) Predator and parasite trait interactions

Finally, to assess how both predator and parasite morphological traits interacted to shape cercariae consumption, we modeled the probability of consumption as a function of each of the three parasite morphological traits and their interactions with the predator's family level head width value. We allowed the parameter to vary based on predator taxon by including a random slope effect for the interaction between scaled head width and predator identity. We included random intercept terms for both parasite and predator taxon identity. This modeling framework allowed us to focus on the independent and interactive effects of the parasite and predator size while accounting for variation in predator traits across taxa. As with the other analyses, we removed individual terms from the initial model, reran the model, and assessed the significance of the terms using log-likelihood test (Bolker 2008).

Results

(i) Variation in parasite consumption among taxa and their associated traits

The proportion of cercariae removed during experimental trials was largely a function of both predator and parasite identity and their associated morphological traits. Across our experiment, particular predators were observed to have removed up to 55% of the administered cercariae whereas other combination only removed 8%. Based on a variance components analysis, roughly 58% of observed variation was associated with predator identity relative to parasite identity (Random intercept-only model: Predator $\sigma^2 = 0.45$; Parasite $\sigma^2 = 0.33$). For predators, taxa in the family Coenagrionidae were the most effective at removing cercariae (mean proportion of cercariae removed ± 1 SE: 0.40 ± 0.03), followed by nymphs in the family Libellulidae (0.28 ± 0.03), Lestidae (0.23 ± 0.03), Aeshnidae (0.20 ± 0.03), and finally insects in the order Ephemeroptera (0.09 ± 0.01) (Supplementary Material Fig. 4). For parasites, the taxa that were most vulnerable to predation were *R. ondatrae* (mean proportion of cercariae removed excluding control treatments ± 1 SE: 0.42 ± 0.04), followed by *Echinostoma* sp. (0.30 ± 0.02), the brevifurcate-apharyngeate cercariae (0.28 ± 0.03), *Australapatemon* sp. (0.18 ± 0.02), and *C. americanus* (0.15 ± 0.02) (Supplementary Material Fig. 2). Overall, we had high recapture of cercariae in the control treatments (with no predators) across all cercariae types (mean proportion of cercariae recaptured: 0.95 ± 0.01, range: 0.91—0.98).

The variation in the consumption ability of predators was correlated with head width, both across taxa as well as *within* family, and the interaction between these sizes (see Table 2). Thus, while predator head width correlated negatively with parasite consumption ability, the strength of this effect varied among taxa. Overall, the probability of predation on a cercaria decreased by 21% for every 1 mm increase in odonate head width *across* all taxa. Across the different families the effect of increasing head width ranged from decreasing consumption by 28% for every 1 mm increase (Coenagrionidae) to a slight increase of 2% in the Aeshnidae (Fig. 1). Since we transformed size metrics into two z-scores, predator head width among taxa were uncorrelated with the variation in size of individual predators. Cercariae from different parasite taxa varied in the consistency of their vulnerability to predation across predator types (Supplementary Material Table 2 for full Tukey HSD results). Within parasite taxa, consumption patterns were largely driven by a couple of dominant consumers, usually led by taxa in the damselfly family Coenagrionidae (Fig. 1).

Among parasites, increases in taxa length (body, tail, and total length) resulted in a higher probability of being

Table 2 Results from generalized linear mixed effects models on the effects of parasite (trematode cercariae) and predator (aquatic insect) traits on cercariae consumption: (i) the effect of predator and parasite traits on cercariae consumption, (ii) the consistency of consumption patterns across predator traits for parasite and predator combinations, (iii) and the interactive effect of parasite and predator traits on cercariae consumption patterns

Model	Variable	Est. $\beta \pm 1$ SE	LL ratio test: χ^2	P value
(i) Trait effects on consumption	Family level head width (scaled)	0.33 ± 0.03	92.58	< 0.001
(i) Trait effects on consumption	Individual predator head width (scaled)	0.32 ± 0.04	135.59	< 0.001
(i) Trait effects on consumption	Family level: individual predator head width interaction (scaled)	0.24 ± 0.03	51.13	< 0.001
(i) Trait effects on consumption	Parasite tail length (scaled)	0.60 ± 0.08	12.22	< 0.001
(ii) Consistency of consumption patterns	Parasite id: Predator id: family level predator head width interaction	See SM table 3	245.58	< 0.001
(iii) Trait interaction	Family level predator head width (scaled): parasite tail length (scaled) interaction	0.23 ± 0.04	138.58	< 0.001

consumed (Table 2). Based on AIC values, using cercaria tail length as the morphological trait resulted in the best-fitting model (Supplementary Table 3). After accounting for variation in predator identity and length, every 100 μm increase in cercaria tail length corresponded to a 30% increase in consumption probability (Table 2) (Fig. 1c). Thus, larger tailed parasites such as *Echinostoma* sp. and brevifurcate-apharyngeate cercariae had a much higher proportion of the administered cercariae removed (proportion cercariae removed ± 1 SE: ECSP: 0.30 ± 0.02, BREVI: 0.28 ± 0.03) compared to the smaller tailed parasites such as *Australapatemon* sp. (AUSP: 0.18 ± 0.02).

(ii) Consistency of consumption patterns across developmental stages

Predators in the suborder Zygoptera (COEN, LEST) tended to have higher variability in consumption across developmental stages, with strong declines in the proportion of cercariae consumed as individuals increased in head width (Supplementary Material: Table 4), although this effect varied greatly across parasite taxa (Fig. 2a, b). In contrast, head width had a weaker effect on the consumption ability of odonates in the suborder Anisoptera (AESH, LIBE), with members of the family Aeshnidae showing a slight increase in cercariae consumption with increases in head width (Supplementary Material: Table 4) (Fig. 2c). Members of the family Libellulidae showed limited variation in consumption ability across the range of head widths in our experiment (Fig. 2d).

Increases in predator head width had especially strong negative effects on the proportion of parasites removed for cercariae of *R. ondatrae* and the brevifurcate-apharyngeate morphotype, (Supplementary Material: Table 4). In contrast, *C. americanus* cercariae showed little variation in the proportion that were consumed in response to variation in odonate head width (Supplementary Material: Table 4),

although this parasite also had the lowest overall consumption of the morphotypes tested. The effects of predator head width on the consumption of both *Echinostoma* sp. and *Australapatemon* sp. cercariae varied with predator identity. For *Echinostoma* sp., the two Zygoptera predators showed substantial reductions in their consumption ability with larger predator head width, whereas no such effect was detected for the two Anisoptera taxa. For *Australapatemon* sp. cercariae, increases in predator head width were either associated with modest increased cercariae consumption (the two Anisoptera taxa), with decreased cercariae consumption (the Zygoptera (LEST), or had no effect (COEN).

(iii) Predator and parasite trait interactions

Key morphological traits of both predator and parasite taxa strongly interacted to shape the predation ability/vulnerability space (See Table 2). Across all predator taxa, cercariae with larger tails were more vulnerable to predation; however, the effect of tail size was dependent on predator head size (Fig. 3). As such, the parasite–predator combinations with the highest consumption involved trials with large-tailed parasites and small-headed predators. Specifically, we observed the highest consumption in trials when the predators were Coenagrionidae, and the prey were *R. ondatrae* or the brevifurcate-apharyngeate cercariae. In contrast, we detected the lowest consumption for trials with our largest predators (Aeshnidae) and one of the smallest cercariae, *Australapatemon* sp.

Discussion

Although parasites can make up a substantial proportion of community biomass and play key roles in ecological food webs (Kuris et al. 2008; Preston et al. 2013), they have been largely omitted from a broader predator–prey framework
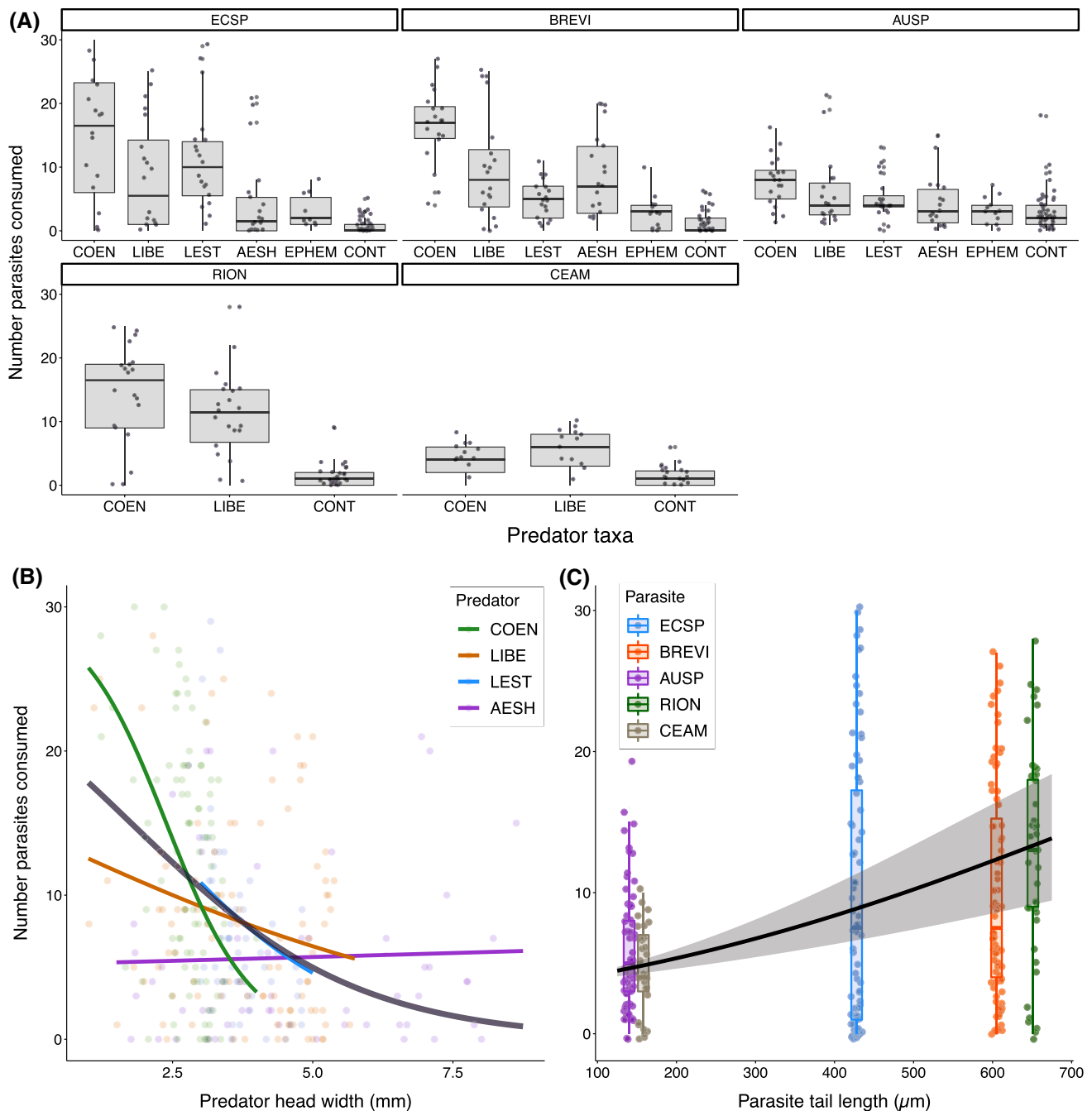
Fig. 1 Consumption patterns of trematode cercariae based on both parasite and predator (aquatic insect) identity, as well as key morphological traits. **a** The importance of predator identity across parasite taxa, with consumption for vulnerable cercariae such as *Ribeiroia ondatrae* (RION, $n = 77$), brevifurcate-apharyngeate (BREVI, $n = 69$) and *Echinostoma* sp. (ECSP, $n = 147$) shaped by high variation across predator taxa, but less so for parasites with low consumption such as *Cephalogonimus americanus* (CEAM, $n = 50$) and *Australapatemon* sp. (AUSP, $n = 148$). **b** Higher consumption of cercariae by preda-

tors with smaller head sizes, but with variation among predator taxa, with stronger negative effect of head size in family Coenagrionidae (COEN, green line and dot, $n = 94$) compared to no observable effect for Aeshnidae (AESH, red line and dot, $n = 58$). **c** Positive association between cercariae vulnerability to consumption and cercariae tail size (scaled parasite tail length: 0.60 ± 0.08, $p < 0.0001$). Each point represents the number of cercariae consumed out of the 30 cercariae administered during an individual predator by parasite trial

such that we lack a general understanding of the traits that determine the likelihood and strength of parasite interactions with non-host taxa, particularly in the context of parasite

consumption. Focusing on parasites with free-living infectious stages in freshwater habitats, we found that consumption of parasites (trematode cercariae) in experimental trials

Fig. 2 Interaction of predator head width size and cercaria tail size on cercariae consumption. For Anisopteran predators (left two squares, Aeshnidae (AESH, $n=58$) and Libellulidae (LIBE, $n=96$)), there was little effect of head size on consumption; Zygopteran predators (two right squares, Lestidae (LEST, $n=51$) and Coenagrionidae (COEN, $n=94$)) showed stronger negative effects of head width size. Effects of head width size were also greater for trematode cercariae (*Ribeiroia ondatrae* (RION, $n=42$), brevifurcate-apharyngeate (BREVI, $n=98$) and *Echinostoma* sp. (ECSP, $n=90$)) observed to have higher vulnerability to consumption. Each point represents the number of cercariae consumed out of the 30 cercariae administered during an individual predator by parasite trial
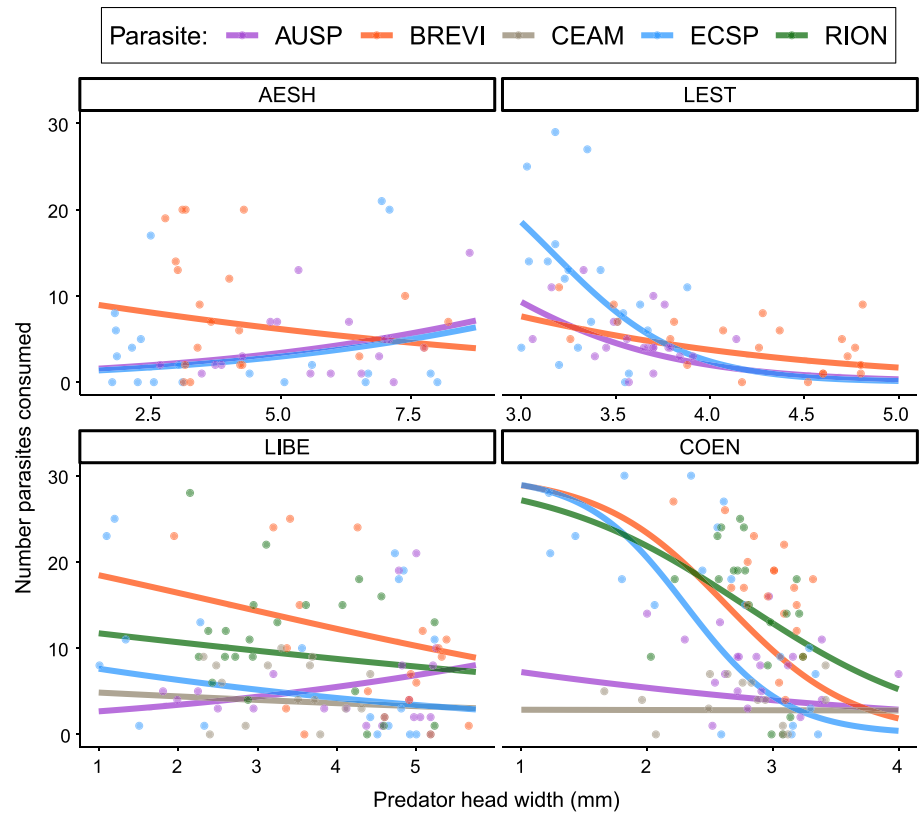
was a function of both predator and parasite morphological traits and taxon identity.

Consumption of parasites across 19 unique combinations of trematode morphotypes and aquatic insect nymphs varied from 55 to 8% of the administered cercariae, for which trials involving relatively large cercariae but small predators led to the greatest consumption values. For instance, small-headed odonate nymphs of the family Coenagrionidae removed ~40% of administered cercariae overall and up to 55% of large-tailed cercariae. In contrast, we were able to recover 95% of administered cercariae across all control (no predators) trials. While previous research has illustrated how predators can effectively reduce transmission of infectious stages to downstream hosts in parasite life cycles (Thieltges et al. 2008; Orlofske et al. 2012), these results help to identify combinations of predator and parasite traits leading to a greater likelihood of consumption.

A key step in elucidating the extent to which free-living infectious stages serve as prey items is to consider how variation in predator size—both among as well as within taxa—controls the likelihood of cercariae consumption. While there was a strong negative effect of predator head width on cercariae consumption at the taxon level, the effect of head width within specific predator taxa varied greatly, such that head size had negative effects within some odonate families but little to no effects in others (Fig. 1b). A potential key driver in the observed pattern

of larger headed taxa not readily consuming cercariae is increased difficulty in capturing small prey with their larger mouths. A cercaria's small size can make it hard for an odonate to grasp with its mouth, which uses a prehensile mask to grab on to prey.

In addition, the observed variation in the effect of head width on consumption across odonate families is likely driven by both variation in foraging strategy and preferred prey type among them. For example, the odonate family with the weakest effect of varying head width on consumption was Aeshnidae, which was the lowest overall consumer of parasites. Taxa in the family Aeshnidae are among the most active foraging odonate taxa, strongly preferring larger prey such as small macroinvertebrates (Corbert 1980), and thus likely do not perceive cercariae as suitable prey, even during early developmental stages. In contrast, nymphal Libelluli-dae (specifically, *Leucorrhinia intacta*) readily consume cercariae, particularly if the nymphs are relatively small-bodied (Catania et al. 2016). While there is typically an optimal predator–prey size ratio that influences their interactions (Weitz and Levin 2006), predatory strategies could also play a role. For instance, foraging at a constant velocity provides the greatest relative energetic benefit for piscivorous fish, but is restricted to small prey, whereas an ambush strategy is best when at smaller predator–prey size ratios (Harper and Blake 1988). In the current study, nymphs of certain taxa may have largely ignored cercariae of a particular size
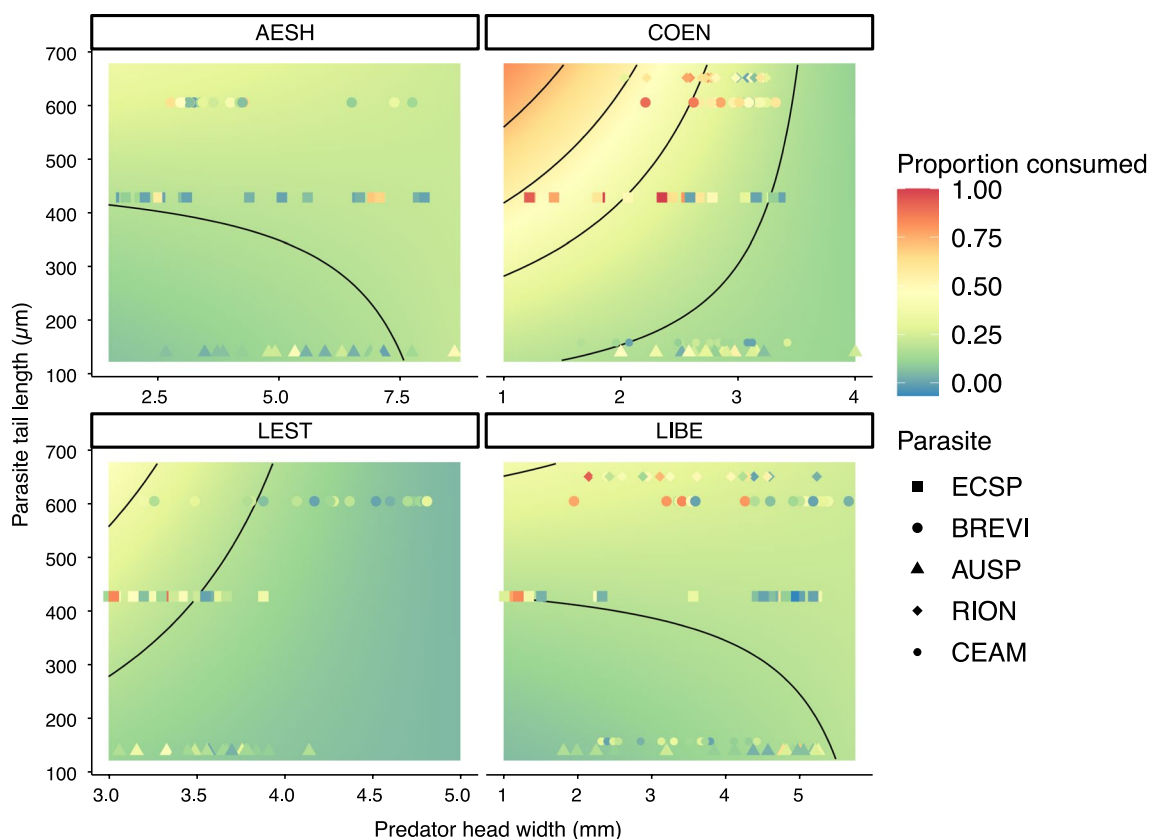
Fig. 3 Effects of predator (nymphal odonate) head size, cercarial tail size and their interaction on the number of trematode cercariae consumed. Points represent predator head width and parasite tail size for each predator by parasite combination, with shapes indicating different parasite taxa. The number of cercariae consumed are represented by a color-based heatmap (warmer = higher consumption, and cooler = lower consumption). The four Odonata predators varied in their consumption ability, but there was more consumption by smaller-headed predators, and on larger tailed cercariae (scaled parasite tail size: 0.54 ± 0.08, $p < 0.0001$; scaled predator head width: -0.28 ± 0.21; $p = 0.184$; tail size: head width interaction: -0.23 ± 0.04, $p < 0.0001$). The heatmap and contour lines indicate the expected consumption patterns for the trait space that was explored in the experiment

based on a combination of predator size and inherent foraging tactics.

Alongside predator morphology, variation in prey behavior and morphology also affect the likelihood of consumption (Klecka and Boukal 2013; Gaeta et al. 2018). By exposing cercariae of multiple, distinct morphotypes to a range of different predators, we observed high variation in predator vulnerability that correlated positively with tail size. Thus, larger cercariae, such as the brevifurcate-apharyngeate morphotype, were up to 4× more vulnerable than smaller cercariae such as those of *C. americanus*. Similarly, in testing the capacity of fish and nymphal damselflies to consume trematodes, Orlofske et al. (2015) found that larger-bodied cercariae (> 1000 μm) were more readily consumed. As cercariae are similar in size to small zooplankton (Morley 2012), it is not surprising that tail size is a key morphological trait in determining vulnerability to odonate predators. As nymphal odonates are highly visual predators (Bybee et al. 2012), larger tailed cercariae are likely easier to perceive prey items

(Fig. 1c). For the taxa in our study, cercaria tail size strongly correlated with swimming behavior, with more active swimming patterns observed in cercariae with larger tails compared to those with smaller tails that engaged in intermittent bouts of activity (McCarthy et al. 2002; Selbach et al. 2019). Thus, the pattern of larger cercariae being more susceptible to predation was likely driven by both higher detectability and higher encounter rates due to the larger size and greater swimming activity.

Due to the correlation between cercariae size and swimming behavior in our study, we are not able to disentangle the primary driver of this observed relationship. However, unraveling size-based morphological features with behavior or other traits is a crucial next step in developing a more predictive understanding of what drives parasite consumption. For instance, as the tails are the most active part of cercariae, and represent large storage sites for glycogen (Fried et al. 1998), tail size likely affects the energetic value of these prey. It is also important to note that large-tailed

cercariae may represent an especially valuable prey item for small-bodied predators because cercariae contain glycogen and essential fatty acids, but lack the tough chitinous exoskeleton typical of most zooplankton (McKee et al. 2020). Small-bodied larval odonates may thus particularly consume large-tailed cercariae if other zooplankton (e.g., *Daphnia*) of similar size are more difficult to digest, thereby reducing net caloric intake.

Building from interactions between predators and prey in free-living systems, such as zooplankton and fishes (Brooks and Dodson 1965; Post et al. 2008), the consistency or volatility of predator preference for a given prey type has important implications for its interactions within the community (van Leeuwen et al. 2013; Nakazawa, 2015). Here we show that the capacity of nymphal odonates to consume cercariae varied through their growth or ontogeny, with the strongest predatory interactions occurring in the smallest (youngest) development stages, which dropped off rapidly as predators grew larger (Fig. 2). This effect was strongest in the Odonata families with the highest mean cercariae consumption; thus, the taxa Coenagrionidae and Lestidae were likely to exhibit shifts in dietary preference with developmental age in natural settings (Catania et al. 2016; Rudolf, 2020). For these taxa, the highest cercariae consumption occurred within trials for which the predators had a head width of < 3.5 mm and < 2.5, respectively, which was observed in under 25% of the individuals of these two families. This implies that the importance of this feeding interaction in natural systems may be highly sensitive to phenological overlap between early staged predators and the availability of cercariae, consistent with patterns found for interactions between zooplankton and planktivorous fishes (Cushing 1990). We thus expect high interaction potential to occur in years or habitats that promote high phenological overlap between early instar predators and free-living parasite taxa (Asch et al. 2019).

An important next step to fully integrate predator–parasite interactions into the broader predator–prey literature is to understand how these consumption patterns shift with increased prey densities, and to scale up simple predation experiments to more complex controlled studies that more closely mirror natural communities. Understanding variation in a predator's feeding rate across a gradient of free-living parasite prey densities can provide valuable insight into the strength and stability of these interactions (Skalski and Gilliam 2001; Coblentz and DeLong 2020). Furthermore, assessing how predators respond to varying free-living parasite densities will enable researchers to disentangle the mechanisms that shape feeding rate by partitioning variation in prey consumption to either variation in the predator's attack rate or its prey handling time (Coblentz and Delong 2020). While simple predator–prey experiments provide valuable insight into these interactions, it is vital to assess how these interactions change under more complex environments

to better understand the likelihood and strength of these interactions in natural systems. By utilizing controlled experiments that include alternative prey items, as well as the addition of interacting taxa such as conspecifics, we can more precisely gauge the interaction strength between predators and free-living parasite prey. Future work should also include cercariae from other trematode taxa that may help to disentangle the relative importance of cercaria size and morphology versus behavior.

A key challenge in the study of predator–parasite interactions is to identify the degree to which predators can limit transmission success by parasites dependent on free-living infectious stages (Johnson et al. 2010; Rohr et al. 2015). Our results highlight the potential for predators to remove a substantial fraction of trematode cercariae during even short (1 h) trials. Given the potential for cercariae to cause pathology in downstream hosts, predator-mediated changes in infection success have important implications for disease in natural systems. For instance, *R. ondatrae,* one of the more vulnerable cercariae in our experiment, is known to be a highly pathogenic parasite for its second intermediate host (amphibians), with high levels of parasite-induced mortality and malformations in infected hosts in an intensity-dependent manner (Wilber et al. 2020). Thus, natural communities with high abundances of aquatic predators may reduce *R. ondatrae* transmission to infection levels that facilitate high amphibian host survival and normal development.

However, as the presence of cercariae in natural systems will likely show high spatiotemporal aggregation within any given habitat, the capacity of predators to reduce transmission will be dependent on both their ability to detect and track cercariae, as well as their functional response to increases in prey densities. Thus, in order to both better understand how predators can reduce infections agents and to continue integrating parasites into the larger predator prey literature, it is vital to assess the functional response of parasite predators to increasing densities of parasites as prey (Born-Torrijos et al. 2021), but also to consider spatiotemporal variation in parasite abundance and the presence of alternate prey (Catania et al. 2016; Schultz and Koprivnikar 2019). Furthermore, predators can also reduce host density through predation (Packer et al. 2003), or alter the behavior of hosts that alter their susceptibility to parasite infection (Duffy et al. 2011; Bertram et al. 2013). Thus, quantifying how predators shape disease patterns requires a net assessment of the multiple, concurrent pathways through which predation can alter transmission.

While interest in the roles of parasites within food webs and ecosystem processes has steadily grown, substantially more research is needed to understand how both intra- and interspecific trait variations alter predator–parasite interactions. Here, we demonstrated that the potential value of cercariae as prey was strongly shaped by both parasite

and predator traits, for which strong feeding interactions were maximized within narrow predator developmental windows based on head width. Thus, a pressing area of research is to understand spatiotemporal variation in the importance of free-living parasite stages as a prey resource, including how phenological synchrony between parasites and predators impact consumption patterns and ultimately regulate downstream parasite transmission. Infectious propagules might also serve as an important source of energy and nutrients, either through direct consumption or through detrital pathways. Future work should thus broadly consider the numerous influences on, and implications of, consumption of free-living infectious stages to understand parasite roles in ecological communities and ecosystems.

Declarations

Conflict of interest The authors declare no conflict of interests.

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