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Trematode parasites exceed aquatic insect biomass in Oregon stream food webs

Daniel L. Preston[1] | Tamara J. Layden[2] | Leah M. Segui[3] | Landon P. Falke[1] | Sara V. Brant[4] | Mark Novak[3]

[1]Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

[2]Department of Biology, Reed College, Portland, OR, USA

[3]Department of Integrative Biology, Oregon State University, Corvallis, OR, USA

[4]Museum of Southwestern Biology, Division of Parasites, Department of Biology, University of New Mexico, Albuquerque, NM, USA

Correspondence
Daniel L. Preston
Email: daniel.preston@wisc.edu

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Abstract

1. Although parasites are increasingly recognized for their ecosystem roles, it is often assumed that free-living organisms dominate animal biomass in most ecosystems and therefore provide the primary pathways for energy transfer.
2. To examine the contributions of parasites to ecosystem energetics in freshwater streams, we quantified the standing biomass of trematodes and free-living organisms at nine sites in three streams in western Oregon, USA. We then compared the rates of biomass flow from snails *Juga plicifera* into trematode parasites relative to aquatic vertebrate predators (sculpin, cutthroat trout and Pacific giant salamanders).
3. The trematode parasite community had the fifth highest dry biomass density among stream organisms (0.40 g/m^2) and exceeded the combined biomass of aquatic insects. Only host snails (3.88 g/m^2), sculpin (1.11 g/m^2), trout (0.73 g/m^2) and crayfish (0.43 g/m^2) had a greater biomass. The parasite 'extended phenotype', consisting of trematode plus castrated host biomass, exceeded the individual biomass of every taxonomic group other than snails. The substantial parasite biomass stemmed from the high snail density and infection prevalence, and the large proportional mass of infected hosts that consisted of trematode tissue ($M = 31\%$ per snail).
4. Estimates of yearly biomass transfer from snails into trematodes were slightly higher than the combined estimate of snail biomass transfer into the three vertebrate predators. Pacific giant salamanders accounted for 90% of the snail biomass consumed by predators.
5. These results demonstrate that trematode parasites play underappreciated roles in the ecosystem energetics of some freshwater streams.

KEYWORDS

biomass, consumer–resource interaction, energy, food web, trematode

1 | INTRODUCTION

Despite being inconspicuous, parasites are increasingly recognized for their potential to directly or indirectly influence ecosystem structure and functioning. Indirect ecosystem effects of parasites are typically mediated by changes in the densities or traits of functionally important host populations (Buck, 2019). For instance, viruses can indirectly regulate marine carbon cycling through changes in the densities of phytoplankton (Talmy et al., 2019); forest pathogens can alter terrestrial nutrient cycling and primary production via

tree mortality (Cobb et al., 2013; Flower & Gonzalez-Meler, 2015); and helminth worms can increase methane emissions from livestock through disease-driven changes in host traits (Fox et al., 2018). Alongside such host-mediated indirect effects, parasites can also directly act as sinks or sources for the transfer of energy, carbon or nutrients through ecosystems (e.g. Kuris et al., 2008). Such direct effects of parasites on ecosystem processes are less commonly recognized and quantified than their indirect effects, and are most likely to occur when parasites attain a significant population-level biomass relative to other organisms in an ecosystem (Preston et al., 2016).

A small but growing number of studies have quantified the biomass of parasites alongside free-living organisms at an ecosystem scale (Kuris et al., 2008; Lagrue & Poulin, 2016; Paseka, 2017; Preston et al., 2013). In estuaries and freshwater ponds, parasite biomass can equal or exceed that of functionally important free-living community members, suggesting that substantial amounts of energy can move directly through parasite populations (Kuris et al., 2008; Preston et al., 2013). The production of free-living parasite stages in aquatic ecosystems can also reroute energy from hosts into other components of the food web (Fong et al., 2019; Thieltges et al., 2008). Parasites are typically rich in nutrients, can be highly productive and are consumed by a diversity of predators, emphasizing the potential for parasites to play important roles in fluxes of energy and matter through food webs (Johnson et al., 2010; Kaplan et al., 2009; McKee et al., 2020; Orlofske et al., 2015; Thieltges et al., 2013).

Freshwater streams can be rich in parasites (Grabner, 2017; Hernandez et al., 2007) and have been central to advancing the understanding of food webs and ecosystem energetics (e.g. Fisher & Likens, 1973; Nakano & Murakami, 2001; Odum, 1957; Power et al., 2008). Yet only recently have parasites been integrated into studies of stream energy flow or trophic ecology. For instance, a compelling series of studies have shown that nematomorph worms increase energy flow from temperate forests into stream food webs by manipulating infected cricket hosts to enter the water (Sato et al., 2019). Parasite-driven subsidies in this system entail an estimated 60% of the annual energetic intake of endangered trout, leading to cascading effects on benthic invertebrates and primary production (Sato et al., 2011, 2012). In New Jersey Pine Barrens streams food webs, parasites are also prominent (Hernandez & Sukhdeo, 2008), although their cumulative biomass is lower than in some other aquatic ecosystems, potentially due to differences in community composition and aquatic productivity (Paseka, 2017). These studies challenge the assumption that energy flux in streams is always dominated by trophic interactions among free-living organisms.

In the present study, our goal was to examine the implications of parasite populations for energy flow in freshwater streams in western Oregon, USA. First, we quantified the biomass densities (biomass per unit area) of aquatic free-living consumers and trematode parasites in three streams. Second, we estimated transfer rates of biomass from *Juga* host snails into both trematodes and free-living aquatic predators (fishes and salamanders). We focused on trematodes because this group dominates aquatic parasite biomass in some lentic and marine ecosystems (Kuris et al., 2008; Lagrue & Poulin, 2016; Preston et al., 2013). Within the study streams, freshwater snails *Juga plicifera* can exceed 90% of the community-level invertebrate biomass and exert strong effects on benthic community structure and primary production (Hawkins & Furnish, 1987). We therefore predicted that aquatic trematode biomass in *Juga* snails could be high due to high host biomass (Lagrue & Poulin, 2016). We were also interested in how rates of snail biomass transfer compared between trematode parasites and aquatic predators because comparable rates would suggest an important functional role for trematodes relative to free-living stream consumers.

2 | MATERIALS AND METHODS

2.1 | Study system

Our study focused on Berry, Oak and Soap Creeks within Oregon State University's McDonald-Dunn Research Forest northwest of Corvallis, Oregon, USA (see Preston et al., 2018 for a map). We sampled three reaches (~45 m long) in each of the three streams, for a total of nine sites. Each reach contained at least two pools and two riffles. The study sites are second-order streams (~1 to 3 m wide in summer) and flow through mixed coniferous forest before entering tributaries of the Willamette River. The three streams support reticulate sculpin *Cottus perplexus*, coastal cutthroat trout *Oncorhynchus clarkii clarkii*, Pacific giant salamanders *Dicamptodon tenebrosus*, brook lamprey *Lampetra richardsoni* and a species-rich macroinvertebrate community (>325 taxa; Anderson & Hansen, 1987). The *Juga* snails in Berry, Oak and Soap Creeks belong to the *Juga plicifera* clade (Campbell et al., 2016; Strong & Whelan, 2019).

2.2 | Free-living biomass

Estimates of standing biomass density were based on stream survey data collected over the summer (June and July). To quantify the composition, density and body sizes of aquatic macroinvertebrates, we used 10 replicate Surber samples (each 0.093 m^2 in area) that were evenly spaced along each stream reach. Invertebrates were preserved in 70% ethanol, measured for body length (mm) and identified to family in the laboratory (Merritt et al., 2008). We additionally quantified *Juga* snail densities and sizes using quadrats (0.25 m^2) randomly placed along the stream bottom. Snails from 10 to 26 quadrats were quantified per stream reach, with higher numbers of quadrats used at sites with low snail densities. All snails were removed from each quadrat by hand and measured for maximum shell length (mm).

Surveys of fishes, salamanders and crayfish were conducted by a crew of four researchers using a backpack electroshocker (Smith-Root LR20B), a block net (1.0 × 1.0 m) and two dip nets (0.30 × 0.25 m). Captured individuals were measured for body length and wet mass in the field. Each reach was systematically shocked on

one pass and densities of organisms were then adjusted by estimated catch efficiencies based on previously performed mark–recapture studies or three-pass electroshocking conducted in each stream (see Appendix for details).

The standing biomass densities of free-living organisms were estimated by converting individual body lengths to dry biomass using length-to-mass regressions (benthic invertebrates) or wet-mass to dry-mass conversion ratios (crayfish, fish and salamanders; Table S1). For *Juga* snails, we developed a regression by measuring, drying and weighing the tissue mass of 172 field-collected individuals ranging from 3 to 34 mm in shell length. For other invertebrate taxa, we used regressions from the literature (Table S1). Snail biomass density estimates exclude shell weight.

2.3 | Trematode biomass

At each of the nine stream reaches, we collected, measured (maximum shell length) and dissected between 106 and 245 *Juga* snails ($M = 151$; Table S2). Snails measured between 1 and 30 mm in shell length (Table S2). All trematodes observed during dissections were grouped into cercarial morphotypes and compared to local species from *Juga* snails described in the literature (Bennington & Pratt, 1960; Burns, 1961; Burns & Pratt, 1953; McCauley & Pratt, 1961; Meade & Pratt, 1965; Pratt & McCauley, 1961). To further aid identifications, we also sequenced 28S ribosomal DNA from representatives of each morphotype and compared them to sequences in GenBank (see Appendix for details). Representative trematode samples were deposited in the Museum of Southwestern Biology at the University of New Mexico and sequences were submitted to GenBank (Table S3).

To quantify trematode standing biomass, trematode tissue and snail tissue were separated with forceps on a subset of infected snails under a dissecting microscope ($M = 15$ snails per trematode morphotype; Table S4). Snail and trematode tissue were dried separately on a 25-mm aluminium dish for 24 hr at 75°C and then weighed on a microbalance (following Preston et al., 2013). We then extrapolated proportional trematode biomasses from individual infected snails to the population level. To do so, we first analysed snail infection status (infected/not infected by any trematode) as a function of shell length using logistic models for each stream reach. Each snail in the field survey quadrats was then assigned an estimated infection status based on the outcome of a Bernoulli trial using the reach- and size-specific infection probabilities from the logistic models. For snails assigned a status of infected, we then applied the mean proportional trematode biomass (% of host tissue from dissections) to each individual snail. We subtracted that same proportion from the snail's estimated biomass. The estimated trematode biomasses per snail were summed across all snails within each quadrat to generate reach-level estimates of trematode biomass density. Because trematodes castrate their host snails, we also estimated the biomass of the 'extended phenotype' of trematodes, which was defined at the combined trematode plus castrated host snail tissue biomass (Dawkins, 1982; Kuris et al., 2008).

We analysed how trematode biomass was related to host snail biomass at both the individual host and population levels. A linear model with log-transformed proportional trematode mass per dissected snail was used to test for the effects of host size (shell length) and trematode taxon identity. We used likelihood ratio tests to test the significance of each predictor. To test how trematode biomass was related to *Juga* snail biomass at the population level, we used a linear mixed effects model with trematode biomass as the response variable, snail biomass as the predictor variable, and a random intercept for stream identity. We also estimated the slope of a linear regression between snail and trematode biomass on a log–log scale to see how the slope compared to predicted host-parasite biomass scaling relationships (e.g. Hechinger, 2013; Lagrue & Poulin, 2016).

2.4 | Biomass flux from snails into vertebrate predators

We estimated the biomass flux from *Juga* snails into Pacific giant salamanders, cutthroat trout and reticulate sculpin using diet data that was collected in summer (June/July), fall (September) and spring (April; see Falke et al., 2020; Preston et al., 2019). Stream predators were collected during electroshocking, as described above. After capture, fish and salamanders were anesthetized with AQUI-S (Silbernagel & Yochem, 2016), lavaged to obtain stomach contents and then released after a recovery period in aerated stream water. Preserved stomach contents were identified and measured for body size in the laboratory under a dissecting microscope. The flux estimates were based at the stream level because the numbers of snails recovered from predator stomachs were too low to estimate fluxes for each separate reach.

Following Preston et al. (2018), Preston et al. (2019), we estimated per capita predator feeding rates on *Juga* snails as

$$\widehat{f}_i = \frac{n_i}{p}\frac{1}{d_i}, \tag{1}$$

where $\widehat{f}_i$ is the population-level mean feeding rate for each predator species (i.e. *Juga* consumed predator^{-1} time^{-1}), n_i is the number of *Juga* snails found in a sample of p predator stomachs and d_i is the estimated *Juga* prey identification time in the gut of the predator. The number of *Juga* snails consumed per predator (n_i) was obtained from the diet surveys described above. The *Juga* prey identification times (d_i) were estimated by feeding *Juga* snails to replicate predator individuals in the laboratory and then lavaging them over time, varying water temperature, predator body size,and prey body size across replicates (see Appendix and Preston et al., 2017 for details). In brief, the prey identification times from the laboratory trials were analysed as a function of the covariates using survival analyses (Klein & Moeschberger, 2005). The resulting functions were then used to estimate the prey identification time for each snail observed in the predator stomachs from the field surveys, using the covariate values for predator and prey sizes, and the stream water temperature. Rates of *Juga* biomass flow into

predators were estimated on a yearly time-scale (g m^{-2} $year^{-2}$) using the densities of predators from electroshock surveys, the estimated predator-specific feeding rates (Equation 1) and the estimated masses of the *Juga* snails observed in the predator stomachs (see Discussion for additional comments on the time-scales of estimates). We generated 95% confidence intervals for the estimates per stream, per predator species and into all predators combined based on the variation in feeding rates, predator densities and prey mass assuming univariate Gaussian errors in each.

2.5 | Biomass flux from snails into parasites

To estimate the rates of biomass flow from *Juga* snails into trematodes, we first estimated an average rate of infection by all trematodes combined for the snail populations in each stream. The rarity of some trematode taxa prevented us from generating species- or reach-specific infection rates. Our estimates thus reflect mean trematode community-level biomass fluxes per stream. The rate of infection is defined as new infections $host^{-1}$ $time^{-1}$ (consistent with the 'Force of Infection' in disease models; Heisey et al., 2006). Rates of infection were estimated using infection hazard models that were fit to relationships between host age and observed infection prevalence (following Heisey et al., 2006). We estimated snail ages based on shell length by adapting a growth rate function originally derived for a closely related species, *Elimia* (=*Goniobasis) proxima* (Stiven & Walton, 1967). The growth rate function was informed by growth data from *Juga* snails that were caged in Oak Creek for a period of 11 weeks spanning summer and early fall (see Appendix for details). We examined the sensitivity of our final biomass transfer estimates to the snail growth rates by varying the estimated snail ages (and hence growth rates) in each stream reach by 1, 2 or 3 standard deviations from their estimated mean and calculating the resulting change to the estimated biomass flux from snails to trematodes (Table S5). To estimate infection rates, we used the Akaike information criterion (AIC) to compare the relative performance of three infection hazard models entailing hazard functions corresponding to (a) a constant infection rate over host age (exponential hazard), (b) an infection rate that is hump-shaped with respect to host age (log-logistic hazard) and (c) an infection rate that either increases or decreases with host age (Weibull hazard). To estimate the number of new infections per time, we applied the top-performing infection hazard model across the susceptible individuals observed in the field surveys in each stream (i.e. the snails assigned a status of uninfected based on the logistic models described in the trematode biomass quantification section above). In all three streams, the Weibull hazard provided the best fit to the age-prevalence data. The AIC values, model parameters and infection hazard plots are provided in the Appendix (Table S6; Figure S1). The estimated number of new infections in the susceptible population within each stream was then converted into a biomass flux (g m^{-2} $year^{-2}$), assuming that each infection reached the average observed trematode biomass per snail based on the dissection data. Confidence intervals for flux rates into trematodes for each stream were constructed using the estimated variation in infection rates and the trematode biomass per infected snail.

3 | RESULTS

3.1 | Free-living and trematode biomass

The free-living animal biomass within all three streams was dominated by *Juga* snails (Figure 1). The mean reach-level *Juga* dry biomass density (3.88 g/m^2) exceeded the combined mean biomass density of all other aquatic organisms (3.13 g/m^2). Reticulate sculpin (1.11 g/m^2), cutthroat trout (0.73 g/m^2), signal crayfish (0.43 g/m^2) and Pacific giant salamanders (0.20 g/m^2) had the next highest biomass densities among the free-living organisms. The combined biomass density of benthic macroinvertebrates, including crayfish, was over five times lower than the *Juga* snail biomass. *Juga* densities averaged 207 snails/m^2 (range = 83 to 327 snails/m^2 across streams).

Six trematode morphotypes were found in the 1,362 *Juga* snails that were dissected from the three streams (Figure 2). Based on molecular data, the six morphotypes were consistent with: Microphalloidea (56.2% of all infections), *Nanophyetus salmincola* (14.8%), Hemiuroidea (9.3%), *Plagioporus* sp. (5.5%), *Metagonimoides oregonensis* (5.5%) and Aporocotylidae (0.3%; see Appendix for further comments on taxonomic identities). Total infection prevalence was 8.6% (Berry Creek),

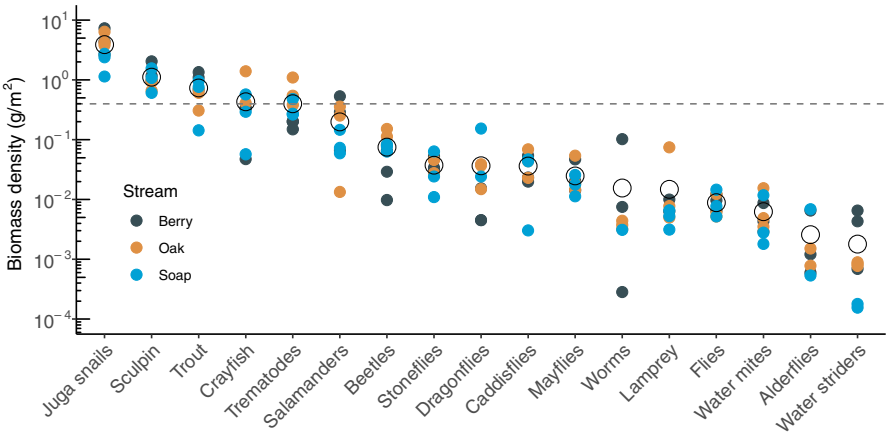

FIGURE 1 Biomass densities of trematode parasites and free-living aquatic organisms from three Oregon streams. The hollow points represent the mean values for each stream and the filled points are three individual reaches within each stream. The dashed horizontal line indicates the mean trematode biomass density

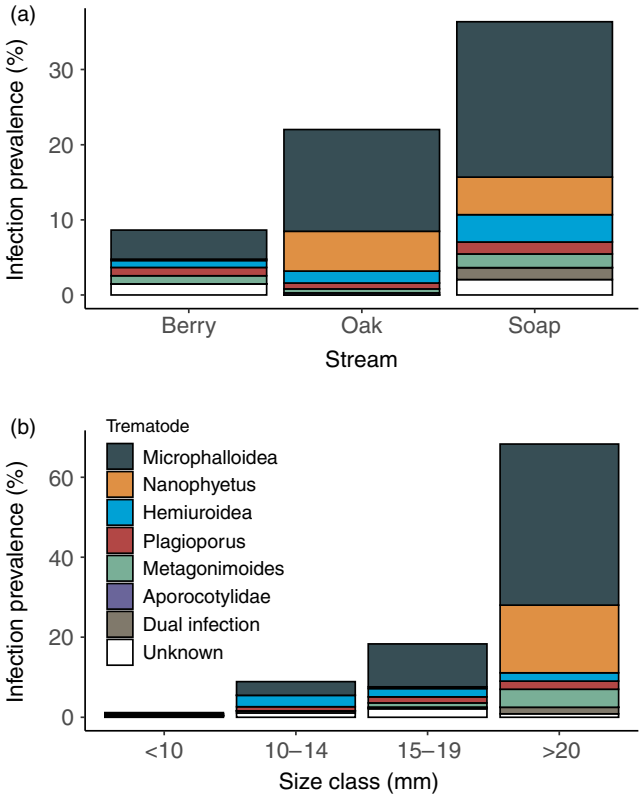

FIGURE 2 The trematode infection prevalence in *Juga* snails across streams (a) and infection prevalence by snail size class (b). Each filled bar either represents a different trematode taxon, dual infections with two trematode taxa or unidentified pre-patent infections. The trematode taxa include the superfamily Microphalloidea, the species *Nanophyetus salmincola*, the superfamily Hemiuroidea, the genus *Plagioporus*, the species *Metagonimoides oregonensis* and the family Aporocotylidae (see Appendix for additional notes on trematode identifications)

22.0% (Oak Creek) and 36.4% (Soap Creek), with all three streams having relatively similar trematode community compositions (Figure 2a; Figure S2). Dual infections were found in 2.4% of infected snails and immature, unidentified infections in 5.8%. Infection prevalence increased strongly with snail size (Figure 2b; Figure S3).

A relatively large proportion of individual infected snails consisted of trematode tissue, which in turn contributed to a high ecosystem level trematode biomass. On average 31.1% of each infected snail was comprised of trematode tissue (range = 17.8% to 45.1% across trematode taxa; Figure S4). The proportional trematode mass differed significantly across trematode taxa ($X^2 = 20.6$, $df = 1$, $p < 0.001$; Figure S4) and increased with host snail size ($X^2 = 8.2$, $df = 1$, $p = 0.004$; Figure S5). The mean reach-level dry biomass density of all trematodes within snails was 0.40 g/m^2, which was exceeded only by *Juga*, both fish species and signal crayfish (Figure 1). The mean trematode biomass density exceeded the combined biomass density of stoneflies, mayflies, caddisflies, dipteran flies, aquatic beetles, dragonflies and true bugs (Figure 1). Trematode tissue represented a mean of 10.4% of the reach-scale snail biomass (4.0% for Berry Creek, 12.4% for Oak Creek and 14.9% for Soap Creek). When considering the extended phenotype of trematodes (i.e. trematode plus castrated snail tissue within infected individuals), the mean biomass density increased to 1.28 g/m^2. The extended phenotype represented 12.8% of total snail biomass at Berry Creek, 40.0% at Oak Creek and 48.1% at Soap Creek.

Trematode biomass was correlated with *Juga* snail biomass at the population level for two of the three streams (Figure S6). There was no clear relationship between snail biomass and trematode biomass across reaches in all three streams combined (LME, $df = 5$, $t = 1.42$, $p = 0.22$). However, when Berry Creek was dropped from the analysis, snail biomass and trematode biomass were positively correlated at the six stream reaches from Oak and Soap Creeks (LME, $df = 3$, $t = 4.21$, $p = 0.02$). For all reaches, the slope of the relationship between trematode and host snail biomass on a log–log scale was 0.41 ($SE = 0.31$). When excluding Berry Creek, the slope was 0.75 ($SE = 0.23$). Berry Creek had a much smaller average snail size than the other two streams (Figure 3; Figure S6).

3.2 | Energy fluxes into predators and parasites

In total, we observed 76 *Juga* snails in the stomachs of 107 Pacific giant salamanders, five *Juga* in 479 trout and 198 *Juga* in 2,068 sculpin that

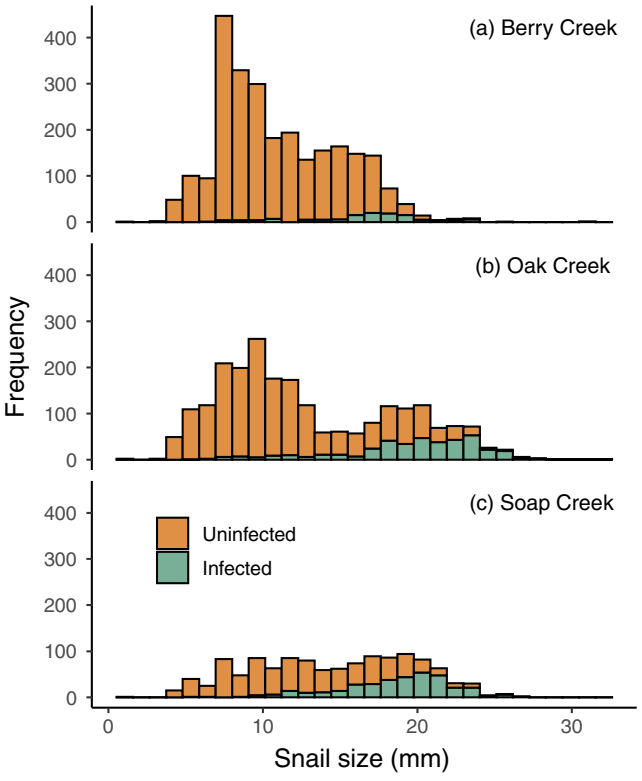

FIGURE 3 Histograms showing differences in the size frequency distributions of *Juga* snails in Berry (a), Oak (b) and Soap Creeks (c). The orange columns show the snails measured in the field and the green columns show extrapolated estimates of the infected snails based on dissection data from a subset of individuals. The numbers of quadrats for which snail density and size distributions were quantified at each stream were 34 at Berry Creek, 43 at Oak Creek and 62 at Soap Creek

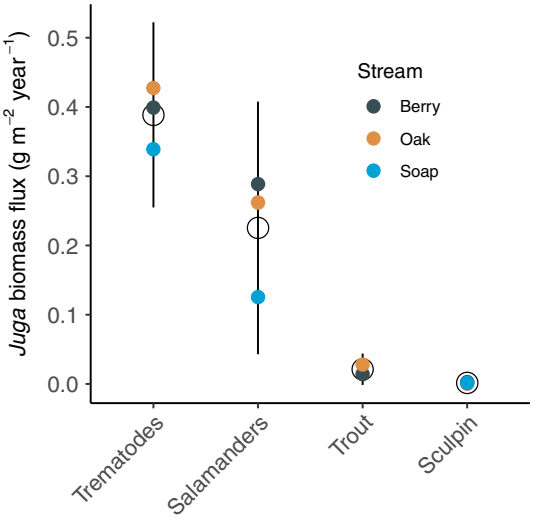

FIGURE 4 The biomass flux from *Juga* snails into trematodes and three aquatic predators. The hollow points represent the mean values for each taxon and the filled points are individual streams. The vertical lines show 95% confidence intervals for the means

were sampled across the three seasons combined. Salamanders represented only 10% of the combined biomass of the three predators and had the lowest density, yet they exhibited the highest feeding rates on *Juga* (1.4×10^{-2} snails salamander^{-1} hr^{-1}) and consumed the largest individual snails (mean snail size = 13.6 mm, *SD* = 7.1). Snail-specific feeding rates for sculpin (1.7×10^{-3} snails sculpin^{-1} hr^{-1}) and trout (1.1×10^{-3} snails trout^{-1} hr^{-1}) were an order of magnitude lower that for salamanders. Sculpin and trout also consumed smaller snails on average (1.4 mm, *SD* = 0.4, and 8.5 mm, *SD* = 7.33 respectively).

Estimated population-level *Juga* biomass fluxes into trematodes in each stream (*M* = 0.39 g m^{-2} year^{-1}; 95% CI = ±0.13) exceeded the estimates for the three aquatic predators combined (*M* = 0.24 g m^{-2} year^{-1}; 95% CI = ±0.18; Figure 4). Biomass fluxes for trematodes were 0.34 g m^{-2} year^{-1} (95% CI = ±0.21) for Soap, 0.43 g m^{-2} year^{-1} (95% CI = ±0.19) for Oak and 0.40 g m^{-2} year^{-1} (95% CI = ±0.28) for Berry Creek. Combined fluxes for the three predators in each stream were 0.13 g m^{-2} year^{-1} (95% CI = ±0.11) for Soap, 0.29 g m^{-2} year^{-1} (95% CI = ±0.40) for Oak and 0.31 g m^{-2} year^{-1} (95% CI = ±0.36) for Berry Creek. Over 90% of the biomass flow from *Juga* into aquatic predators was due to predation by Pacific giant salamanders (*M* = 0.22 g m^{-2} year^{-1}; 95% CI = ±0.18). Sculpin accounted for an average of only 0.0014 g m^{-2} year^{-1} (95% CI = ±0.00075), while cutthroat trout accounted for an average of 0.014 g m^{-2} year^{-1} (95% CI = ±0.022; Figure 4).

4 | DISCUSSION

The streams in our study have a history of ecological research on food webs and patterns of ecosystem energy flow (Warren et al., 1964). Prior work recognized the dominant biomass of *Juga* snails and hypothesized that they strongly affect stream energy flow (Earnest, 1967; Warren et al., 1964). However, the ecological roles of trematodes infecting snails in this system have been largely overlooked. Our results indicate that trematode parasites have a large standing biomass within snail hosts that can exceed many functionally important free-living stream community members, including benthic insects. We additionally show that estimated rates of biomass transfer from snails into trematodes are comparable or exceed the biomass transfer of snails into three aquatic predators. These results collectively suggest that trematodes play an important functional role in the stream ecosystems we studied.

The estimates of standing trematode biomass in the three Oregon streams are the highest reported estimates of parasite biomass density for aquatic ecosystems to our knowledge (see Paseka, 2017 for comparisons among prior studies). If the parasite wet mass estimates from Kuris et al. (2008) are converted to dry mass (assuming DM = 0.1 × WM; Benke, 1984), then the trematode dry biomass density in the Oregon streams exceeds the biomass of all parasite taxa in each California estuary from Kuris et al. (2008). Our trematode biomass density estimates also exceed those from freshwater ponds in California (Preston et al., 2013), New Zealand lakes (Lagrue & Poulin, 2016) and oligotrophic New Jersey streams (Paseka, 2017). Moreover, the trematode biomass estimates would have been slightly higher if we had incorporated life stages infecting non-snail hosts (i.e. miracidia, metacercariae and adult worms in intermediate and definitive hosts), although these stages are typically a small fraction of total trematode biomass (Kuris et al., 2008, Preston et al., 2013, but see Lagrue & Poulin, 2016). Additionally, examining seasonal changes in biomass presents an important topic for future work, as our parasite surveys focused only on summer snapshots.

Host biomass is a primary factor predicted to control parasite biomass. Indeed, variation in host snail biomass across ecosystems helps explain much of the differences in the trematode biomass reported from other ecosystems (Kuris et al., 2008; Lagrue & Poulin, 2016; Paseka, 2017; Preston et al., 2013). Prior work based in metabolic theory predicts that the maximum biomass of endoparasites at carrying capacity should relate to host biomass with a ¾ scaling relationship (Hechinger, 2013; Lagrue & Poulin, 2016; Poulin & George-Nascimento, 2007). Among all of our nine study sites, the slope of trematode biomass regressed against host snail biomass on a log–log scale was 0.41, well-below ¾. However, when one stream (Berry Creek) was removed from the regression, the other six reaches exhibit a relationship with a slope of 0.75 (see Figure S6 for host and trematode biomass relationships). Berry Creek had the lowest trematode biomass and also had a snail population skewed towards smaller individuals than the other two streams (Figure 4a). Berry Creek was also lower in stream flow than the other sites and likely provided a less stable environment in which snail populations are subject to summer die-off events from channel drying, leading to few older individuals in the populations (Diamond, 1982). As a result, we suspect that the snail population at Berry Creek supported a trematode population that was well-below carrying capacity, which may explain the divergence in host–parasite scaling relationships from the other streams.

By sampling predator stomach contents for *Juga* snails, we were able to test the prediction that predation rates on snails by aquatic predators are relatively low (Hawkins & Furnish, 1987; Warren et al., 1964). Of the free-living aquatic consumers sampled, only Pacific giant salamanders consumed a significant quantity of snails (see also Esselstyn & Wildman, 1997; Falke et al., 2020). The large size and robust shells of *Juga* snails prevent their widespread consumption relative to other macroinvertebrate prey. Among the 25 taxa most commonly consumed by reticulate sculpin, *Juga* snails are preyed on at the lowest rates (Preston et al., 2019). Similarly, we only observed five total *Juga* in the 479 trout sampled. These two predator species likely pass most snail shells through their digestive system intact, as they are unable to digest the shells in the laboratory (D. Preston, pers. obs.). We did not estimate the biomass flux of *Juga* snails into signal crayfish at our study sites. Crayfish are snail predators in most aquatic ecosystems (Twardochleb et al., 2013). That said, the shells of pleurocerid snails (e.g. *Juga*) are more difficult to crush than other commonly consumed snail taxa, in some cases leading to low predation rates even by snail specialists (Stein et al., 1984). At our sites, existing data suggest that signal crayfish have relatively low feeding rates on *Juga*. One signal crayfish of 186 that we sampled from Oak, Berry and Soap Creeks contained a *Juga* snail (Segui, 2019). A similar proportion of crayfish contained *Juga* snails (one out of 140) in Berry Creek as reported by Mason (1963). Moreover, large crayfish primarily feed on detritus, algae and allochthonous plant matter (Mason, 1963), and did not consume *Juga* snails in the laboratory unless their shells were first crushed (D. Preston pers. obs.). Nonetheless, the combined estimates of snail biomass flux into aquatic predators are probably slight underestimates due to the omission of crayfish. It is also possible that crayfish consume *Juga* snails without ingesting any shell fragments, making their presence in diet samples challenging to detect (Krist, 2002). Birds or mammals (e.g. racoons) may also consume *Juga* snails, although these trophic links have not been studied to our knowledge. Lastly, some energy from snails will enter the system directly when snails die from causes other than predators and they are consumed by scavengers or decompose.

We estimated comparable rates of biomass flux from snails into fish and salamanders relative to trematodes. Our approach to estimating the biomass flux from host snails into trematodes makes several assumptions that may make our estimates conservative. These include the following: (a) infected and uninfected snails exhibit the same mortality rates; (b) snails do not clear their infections; and (c) the overall size-prevalence curve across all trematode taxa approximates the sum of the infection rates for each individual trematode species. Examining the age-prevalence curves for the trematode community shows that prevalence increases throughout the range of snail ages/sizes (Figure S3). A hump-shaped curve, with prevalence decreasing in the oldest age classes is thought to be indicative of hosts clearing infections and/or infection-induced mortality (Anderson & May, 1979; Cohen, 1973). We did not observe hump-shaped age-prevalence curves in the *Juga* snail infection data. Additionally, infection prevalence approached 100% in the oldest age classes, and infection rates were best approximated by a Weibull model, in which the force of infection increases monotonically with snail age (Figure S1). These observations suggest that mortality and snails clearing their infections were not likely to have played large roles in driving the observed infection prevalence, although we cannot rule out these processes entirely with our observational data. Both processes would result in an underestimation of the infection rates and resulting biomass flux into trematodes. Additionally, we assumed that infection does not strongly affect snail growth rates. Across different systems, trematodes can cause snails to grow slower, faster or have no effect (Sorensen & Minchella, 2001), potentially influencing observed age-prevalence curves (but see Graham, 2003). If infected snails grow more rapidly or more slowly than uninfected snails, our infection rates could be overestimated or underestimated respectively. Effects of infection on snail growth, if they occur, are likely to be specific to each trematode taxon in the assemblage. The grouping of all trematode taxa into a single infection rate estimate also subsumes species-specific infection rates into a community-wide average estimate, possibly omitting biological processes that are specific to each trematode (e.g. variation in infection-induced mortality across trematodes, or trematode–trematode interactions within snails that would affect taxon-specific prevalence).

An important consideration when comparing magnitudes of distinct species interactions is that the time-scales of the processes involved present additional challenges of interpretation. In our study, the infection rate estimates were based on prevalence data in snails that live as long as 7 years. In other long-lived snails, trematode infections can persist up to 4 years (Sousa, 1993) and infection patterns can be remarkably consistent on scales as long as a decade (Byers et al., 2016). In a closely related stream snail *Elimia proxima* hosting some of the same trematode taxa found in our study, infection prevalence did not vary significantly across seasons over the course of 3 years (Zemmer et al., 2017). Based on these observations, the observed infection prevalence of *Juga* snails potentially reflects the outcome of infection events over the span of years, especially in the larger streams with more stable snail populations. In contrast, our predation rate estimates were based on the time span that prey items remain identifiable in predator stomachs (Preston et al., 2017). For *Juga* snails, this averaged around 60 hr, such that diet information reflects foraging over hours to a few days. Because of this difference in time-scales, as well as previously quantified seasonal variation in stream predator feeding rates (Preston et al., 2019), we chose to incorporate diet information over three distinct seasons spanning 1 year, despite basing infection rates on only summer data. We also expressed energy flows for both predators and parasites on a yearly time-scale given that the observational data incorporate intra-annual variation for both interaction types, and potentially inter-annual variation for trematodes. Consideration of these distinct time-scales re-enforces how the temporal resolution of sampling can alter inferences about species interactions (e.g. Novak & Tinker, 2015). In our case, higher temporal resolution data

for predation relative to parasitism is probably warranted, although how sampling frequency affects inferences across species interactions remains unclear.

The ultimate fate of trematode biomass in the streams remains an important question. By assimilating resources that would otherwise go into snail growth and reproduction, trematodes have the potential to divert energy along pathways that may be distinct from predation and other sources of snail mortality. The free-living aquatic larval stages (i.e. cercariae) that are asexually produced by trematodes within snail hosts can have rates of secondary production that equal or exceed co-occurring free-living invertebrates (Kuris et al., 2008; Preston et al., 2013; Thieltges et al., 2008). Only a small fraction of these larval stages successfully infect hosts, with many likely being eaten by consumers (Morley, 2012) including fish, amphibians, zooplankton and benthic macroinvertebrates (e.g. Kaplan et al., 2009; Mironova et al., 2019; Orlofske et al., 2015; Welsh et al., 2017). It is probable that some of the parasite production that would otherwise be locked in *Juga* snail hosts is consumed by various stream organisms as well. For instance, filter-feeding macroinvertebrates (e.g. net-spinning caddisflies, black flies) consume particles in the size ranges of trematode cercariae (Wallace et al., 1977). Furthermore, certain trematodes from our study, such as *Nanophyetus salmincola*, produce seasonal pulses of cercarial stages (Hershberger et al., 2019), potentially providing a temporally varying yet nutrient-rich prey source to certain stream consumers. Quantifying these pathways presents an important area for future work.

Our results add to a growing literature showing that parasites can play important roles in ecosystem processes, including fluxes of energy and matter. Trematodes in *Juga* snails represented the highest biomass density reported from any aquatic ecosystem. Rates of biomass flow from snails into trematodes exceeded rates of snail biomass consumption by predators, suggesting that trematodes may play roles in energy transfer that are comparable to functionally important free-living community members. Future work should aim to elucidate the specific fate of trematode parasite biomass and its functional importance to non-host community members. Additionally, the net result of direct and indirect (host-mediated) effects of parasites on energy flow should be recognized in future work. For example, host snails are usually castrated after infection, hence trematode infection can lead to population-level reproductive decreases on one hand (Lafferty, 1993; Negovetich & Esch, 2008), yet biomass overcompensation may also occur due to reduced intraspecific competition among snails (Preston & Sauer, 2020). Comparing the relative magnitude of direct versus indirect roles of parasites in energy flow presents a promising area for future research.

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AUTHORS' CONTRIBUTIONS

D.L.P. and M.N. conceived the ideas; D.L.P., T.J.L., L.M.S. and L.P.F. collected field and laboratory data; T.J.L. performed trematode biomass measurements; S.V.B. identified trematodes with molecular methods; D.L.P. wrote the first draft and all the authors contributed to revisions and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.sxksn031w (Preston et al., 2020).

ORCID

Daniel L. Preston https://orcid.org/0000-0002-0486-3466

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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