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## Small Estuarine Fishes Feed on Large Trematode Cercariae: Lab and Field Investigations

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**ABSTRACT:** In aquatic ecosystems, dense populations of snails can shed millions of digenean trematode cercariae every day. These short-lived, free-living larvae are rich in energy and present a potential resource for consumers. We investigated whether estuarine fishes eat cercariae shed by trematodes of the estuarine snail *Cerithidea californica*. In aquaria we presented cercariae from 10 native trematode species to 6 species of native estuarine fishes. Many of these fishes readily engorged on cercariae. To determine if fishes ate cercariae in the field, we collected the most common fish species, *Fundulus parvipinnis* (California killifish), from shallow water on rising tides when snails shed cercariae. Of 61 killifish, 3 had recognizable cercariae in their gut. Because cercariae are common in this estuary, they could be frequent sources of energy for small fishes. In turn, predation on cercariae by fishes (and other predators) could also reduce the transmission success of trematodes.

Are parasites at the top of the food chain, or do they themselves have natural enemies? In aquatic habitats with cercariae, many organisms eat zooplankton similar in size and behavior to cercariae. Because cercariae are glycogen-rich zooplankters (Ginetsynskaia, 1960; Xu et al., 1994) they could be suitable prey items. Zooplanktivorous fishes could be a significant source of cercariae mortality and thus decrease transmission to second-intermediate hosts. In addition, cercariae could provide a significant source of energy for these fishes.

The literature on cercaria predation centers on biological control of *Schistosoma mansoni*. Several studies show that guppies and an African killifish (*Poecilia reticulata* and *Epiplatys fasciolatus*, respectively) eat *S. mansoni* cercariae in the laboratory (Rowan, 1958; Pellegrino et al., 1966; Knight et al., 1970; Siau et al., 1992). Oliver-Gonzalez (1946) observed cercariae being consumed by guppies in a Puerto Rican pond. In addition to fishes, several invertebrates readily eat cercariae (of several species) in the laboratory, including turbellarian worms (Holliman and Meham, 1971), copepods (Christensen, 1979; Banerjee, 1996; Schotthoefer et al., 2007), odonates (Schotthoefer et al., 2007), annelids (Fernandez et al., 1991), anemones (Mouritsen and Poulin, 2003), cladocerans, and ostracods (Christensen, 1979).

Correlational field studies have demonstrated a negative association between cercaria predators and transmission to second-intermediate hosts, specifically when these hosts are co-habited by epibionts. Gruffydd (1965) found that cercariae are eaten by the annelid *Chaetogaster limnaei limnaei*, a commensal of fresh-water snails. Rodgers et al. (2005) and Ibrahim (2007) demonstrated that *Chaetogaster limnaei limnaei* actually reduces trematode transmission from its host snail by preying on cercariae. The sea anemone, *Anthopleura aureoradiata*, can protect the cockle it lives on from infection by preying on cercariae as they near the cockle (Mouritsen and Poulin, 2003). However, none of these studies has verified cercaria predation in nature via gut content analysis or considered how cercaria and predator sizes alter predation rates.

We examined cercaria predation by fishes in Carpinteria Salt Marsh (CSM), a 66 ha estuary in southern California. Here the California horn snail, *Cerithidea californica*, serves as the first-intermediate host for a guild of 18 trematodes. Nearly all of these species seek out second-intermediate hosts that can be fishes, crabs, clams, polychaetes, or snails, depending on the species of trematode. Birds are usually the final hosts, and these trematodes complete their life cycles when a bird (or a mammal, such as a raccoon) eats the second-intermediate host. Snails are abundant, and the prevalence of infection with trematodes is high (Lafferty, 1993). This leads to a high biomass density of trematode tissue in the estuary (Kuris et al., 2008). Cercariae are common in the water column (Stevens, 1996; Kuris et al., 2008), and it has been proposed that they are fed on by zooplanktivores, particularly fishes (Lafferty, Hechinger, et al., 2006). We predicted that if fishes commonly prey on cercariae in the wild, then fishes would actively consume cer-

cariae in the laboratory. We also predicted that cercariae might comprise a detectable component of wild fish diets.

We verified that fishes do consume cercariae in a laboratory setting. Then, using our observations that juvenile fishes readily ate cercariae in aquaria, we examined wild-caught juvenile killifish for cercariae in their guts. Our findings confirm that estuarine fishes consume cercariae of most trematode species under laboratory conditions, and that cercaria predation is detectable in the field for the most common fish species in the estuaries of southern California.

We collected *C. californica* from CSM and housed them in mesh bags on a water table in the dark. To induce shedding of cercariae, we placed individual snails in glass scintillation vials containing seawater and exposed them to light for 4 hr. Seven trematode species were investigated: *Acanthoparyphium spinulosum*, *Cloacitrema michiganensis*, *Himasthla rhigedana*, *Himasthla* sp. B., *Parorchis acanthus*, *Renicola buchani*, and *Euhaplorchis californiensis*. Three additional species were used, but only in a single trial: *Probolocoryphe uca*, *Stictodora hancocki*, and *Pygidiopsoides spindalis*. With the exception of *E. californiensis*, *S. hancocki*, and *P. spindalis*, all these trematodes are easily visible to the naked eye.

Six fish species were collected from CSM: *F. parvipinnis* (California killifish), *Clevelandia ios* (arrow goby), *Leptocottus armatus* (staghorn sculpin), *Gillichthys mirabilis* (longjaw mudsucker), *Hypsopsetta guttulata* (diamond turbot), and *Atherinops affinis* (topsmelt). Fish were housed in aquaria with running seawater for at least 1 wk to acclimate them to the laboratory environment and fed fish flakes ad lib. We followed University of California–Santa Barbara guidelines for acquisition, transport, housing, and use of fishes.

Before a feeding trial, the fish were moved to individual 250- or 500-ml Erlenmeyer flasks (depending on fish size) and held without food for 24 hr. Between 30 and 100 cercariae of a single trematode species were offered to each fish for 15–60 min, depending on how long it took each fish to display feeding behavior. Preliminary trials indicated that number of cercariae eaten would not provide a meaningful measure, because most fish simply ate all the cercariae provided. For this reason we chose the simple qualitative measure of whether or not fish actively ingested cercariae. At the conclusion of the feeding trial, each fish was removed from the flask, killed, measured for total length (TL) and dissected immediately to check for the presence of cercariae in the gastrointestinal (GI) tract. We examined the mouth, then excised the GI tract and mounted it on a slide for inspection using a stereomicroscope. For small fish less than 17 mm TL, the GI tract was opened but not excised from the body. Feeding trials included 68 fish. We used logistic regression to evaluate the association between fish feeding and the predictors: cercaria species and size (volume) and fish species and size (TL). All first-order interactions were initially entered, but non-significant effects ( $P > 0.05$ ) were sequentially removed from the model to help preserve power and degrees of freedom.

Soft-bodied prey, e.g., cercariae, are difficult to detect in gut contents because of their rapid digestion rate (Sutela and Huusko, 2000). To assess our ability to detect cercariae in the guts of wild-caught fish, we determined the rate that juvenile killifish digested cercariae in the laboratory. To be certain that we dissected fish that ate cercariae, we observed them feeding through a hole in a black curtain. Fish exhibiting feeding behavior were immediately anesthetized and left in the flask for a 15-, 20-, 25-, or 30-min “digestion” interval, after which they were killed and dissected. The digestion rate trials consisted of 10 fish. We recorded the location of cercariae in the GI tract for each time interval.

We chose to use the California killifish for field investigations based on its high abundance in the estuary (Hechinger et al., 2007) and its ready ingestion of multiple species of trematode cercariae in the laboratory. We selected collection sites where previous surveys indicated a high prevalence of *H. rhigedana* in snails. Killifish readily ate this trem-

TABLE I. Species-by-species results of predation on cercariae by fish. Each entry represents the total number of trials where fish ate cercariae over the total number of trials. A dash indicates that no trials were performed for that fish-trematode combination. Fish species: *Atherinops affinis*, *Fundulus parvipinnis*, *Clevelandia ios*, *Gillichthys mirabilis*, *Hypsopsetta guttulata*, and *Leptocottus armatus*. Trematodes in boldface use fishes as second-intermediate hosts. Trematode species: *Acanthoparyphium spinulosum* (ACAN), *Cloacitrema michiganensis* (CLOA), *Himasthla rhigedana* (HIMA), *Himasthla* sp. B. (HIMB), *Parorchis acanthus* (PARO), *Probolocoryphe uca* (PROB), *Euhaplorchis californiensis* (EUHA), *Pygidiospoides spindalis* (PYGI), *Stictodora hancocki* (STIC), and *Renicola buchanani* (RENB).

Fish	ACAN	CLOA	HIMA	HIMB	PARO	PROB	EUHA	PYGI	STIC	RENB	Total
<i>A. affinis</i>	—	1/1	1/1	—	—	—	0/1	—	—	—	2/3
<i>C. ios</i>	2/2	1/1	1/1	3/4	1/2	0/1	0/3	—	—	—	8/14
<i>F. parvipinnis</i>	0/2	1/3	1/2	2/3	4/5	—	0/6	—	0/1	6/6	14/28
<i>G. mirabilis</i>	0/1	—	1/1	1/3	—	—	—	—	—	—	2/5
<i>H. guttulata</i>	—	2/2	2/2	1/1	1/1	—	—	—	—	1/1	7/7
<i>L. armatus</i>	0/1	2/3	1/2	—	2/2	—	0/2	0/1	—	—	5/11
Total	2/6	7/10	7/9	7/11	8/10	0/1	0/12	0/1	0/1	7/7	38/68

atode in the laboratory experiments. Moreover, it has a large cercaria with a distinctive pigment mass associated with its anterior nerve tissue and thus is relatively easy to recognize in the gut. At CSM we surveyed 61 killifish ranging in size from 15 to 57 mm from July 2006 to September 2006. We targeted juvenile fish during the rising tide when cercariae are shed in the greatest numbers (Stevens, 1996; Fingerut et al., 2003). Fish were collected from channels and mudflats. Captured fish were then dissected in a temporary field laboratory within 25 min of capture. Twenty-five minutes was the cutoff for field dissections based on the digestion rate in laboratory trials, which showed that cercariae were no longer distinguishable after 30 min. For each fish we recorded the collection site, time of collection, daily cloud cover, tidal height, and TL. We partitioned our examination of the GI tract into the foregut (mouth and esophagus) and midgut (stomach). We also recorded the gut contents of the intestine.

In the laboratory all species of fish tested ate cercariae of at least 1 trematode species (Table I). We constructed a logistic regression model to consider the effects of fish species and trematode species on the interaction. The trials with *A. affinis* had to be excluded from this analysis because of low sample size ( $n = 3$ ) as well as the 3 single trials with uncommon trematode species (Table I). In the logistic model, fish species did not affect the outcome of a trial ( $\chi^2 = 7.14$ ,  $df = 5$ ,  $P =$

0.21), but trematode species did ( $\chi^2 = 31.3$ ,  $df = 5$ ,  $P < 0.0001$ ,  $R^2 = 0.57$ ). Fish consistently avoided eating *E. californiensis* cercariae but always consumed *R. buchanani* cercariae (Table I).

Fish size was a significant effect in the logistic regression above, but, because fish species was insignificant, we were able to include the 6 observations excluded in the previous analysis. We also considered whether the significant effect of trematode species could be explained by cercarial size. Since cercariae of *R. buchanani* adhere to each other by their tails ("rattenkönig [rat-king] cercariae"), we chose to represent this species as the combined volume of a clump of 20 cercariae. This is a rough estimate of their variable cluster size (the results were not sensitive to substantial variation in this estimate). We estimated cercaria volumes from published and direct measurements of their bodies and tails and approximated them to simple geometric shapes (Kuris et al., 2008). There were significant effects of cercarial size (log size,  $\chi^2 = 22.6$ ,  $df = 1$ ,  $P < 0.0001$ ) and fish length ( $\chi^2 = 7.1$ ,  $df = 1$ ,  $P = 0.0076$ ) ( $R^2 = 0.32$ ,  $n = 68$ ). In short, consumption was highest on large cercariae (Fig. 1) when consumed by small fish (Fig. 2).

When killifish were isolated in an Erlenmeyer flask under laboratory conditions, they became subdued and required a period of adjustment of 4–6 hr before they would feed. Once acclimated in an Erlenmeyer flask, they hovered near the bottom and remained still. If the fish de-

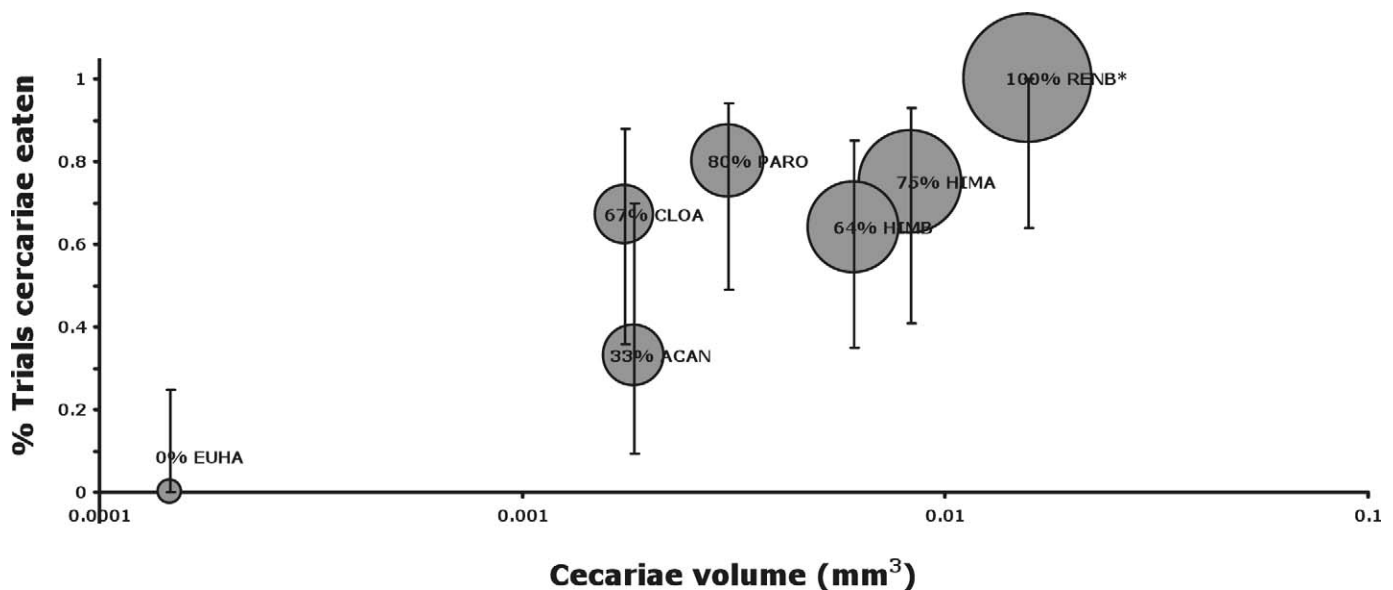


FIGURE 1. The percentage ( $\pm$  95% C.I. calculated for percentages) of trials in which fish ate cercariae, by trematode species and their relative sizes. *Renicola buchanani* (RENB) is depicted as a typical rat-king cluster of 20 cercariae. Cercariae volume is distributed along a log scale. The size of each circle represents how the cercariae volume would look packaged as a sphere. See the Results for the multivariate analysis. Trematode species: *Acanthoparyphium spinulosum* (ACAN), *Cloacitrema michiganensis* (CLOA), *Himasthla rhigedana* (HIMA), *Himasthla* sp. B. (HIMB), *Parorchis acanthus* (PARO), *Renicola buchanani* (RENB), and *Euhaplorchis californiensis* (EUHA).

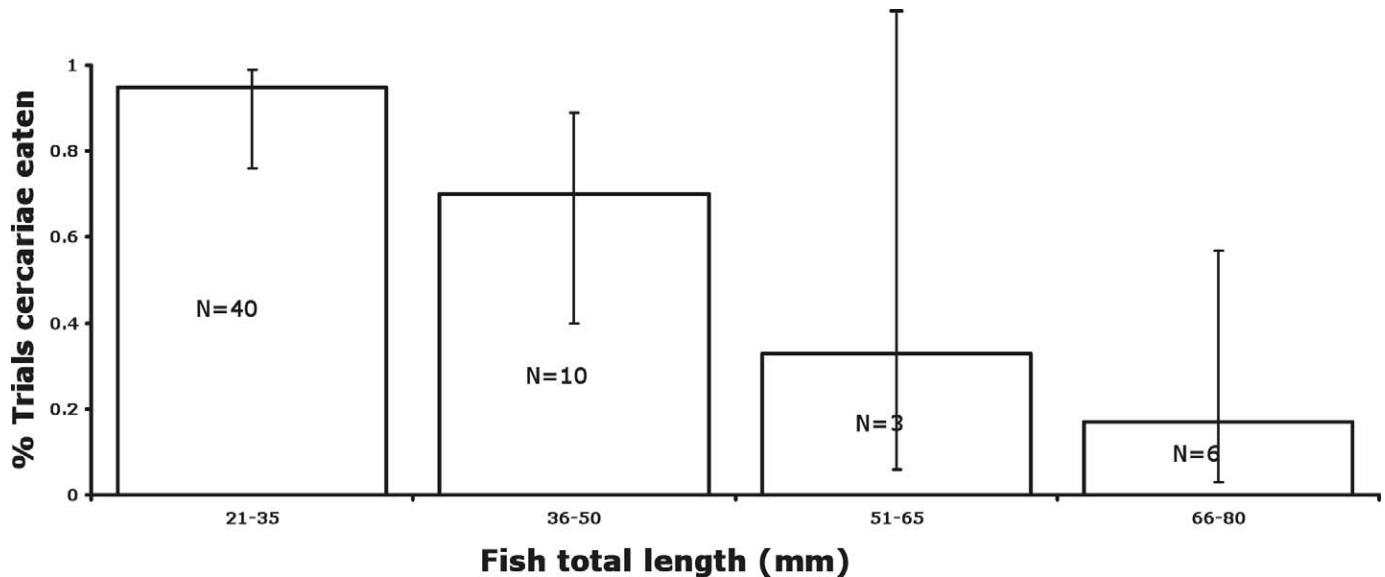


FIGURE 2. The percentage ( $\pm 95\%$  C.I. calculated for percentages) of trials in which fish ate cercariae, by fish total length. All fish species are pooled because fish species was not a significant effect. See the Results for the multivariate analysis also considering fish length.

tected movement, they would become agitated and dart rapidly within the flask, both vertically and horizontally. This behavior lasted for no more than 30 sec before the fish resumed their previous position on the bottom of the flask.

Introduction of pipetted cercariae into the flask stimulated agitated behavior in the fish. After 30–120 sec, the swimming speed decreased and feeding behavior was apparent. Feeding behavior involved fish approaching cercariae and repositioning the body for attack and ingestion. Fishes focused on the movement of cercariae while foraging; they appear to use visual cues to prey on cercariae. The body-repositioning behaviors were often repeated until all cercariae in the flask were consumed. When pure seawater was pipetted into the flask as a control, the fish made a few rapid circles consistent with agitation, and then settled back down to the bottom.

Recently ingested cercariae in the foregut of the fish were readily identifiable to species. *Himasthla rhigedana* cercariae were also identifiable in the midgut by their characteristic anterior pigment mass. With the exception of *H. rhigedana*, cercariae were no longer recognizable after the 25 min it took to pass from the foregut to the midgut.

Of the 61 killifish examined in the field, 3 (5%) had *H. rhigedana* cercariae in their guts. All 3 fish with cercariae in their guts were juveniles from the mudflat habitat. Considering only juvenile killifish from the mudflats, 3/25 (12%) of the fish had cercariae in their guts. The conspicuous appearance of *H. rhigedana* cercariae is a likely explanation for why we found this species, and not others, in wild-caught fishes. Half the fish had identifiable contents in the midgut. Of these, 28 had crustaceans, 16 algae, 7 polychaetes, 7 nematodes, 5 insects, and 5 unidentified eggs.

All estuarine fishes we studied recognized trematode cercariae as food. This was particularly true for small fish feeding on large cercariae. It may be that small cercariae do not represent profitable food items, particularly for larger fishes. The most readily consumed trematode cercariae were those of *R. buchani*. This species has a unique clustering behavior and pink coloration (Martin, 1955) that has been suggested to be an adaptation to facilitate ingestion by fishes that serve as the trematodes' second-intermediate host, *F. parvipinnis* and *G. mirabilis*). Fishes eat clusters of rat-king cercariae more readily than solitary cercariae of the same species (Galaktionov and Dobrovolskij, 2003). Because we found that non-hosts also eat rat-king clusters, this putative adaptation may have a cost. Similarly, several freshwater trematode cercariae mimic mosquito pupae or worms in both morphology and behavior to entice fish second-intermediate hosts to prey on them (Dronen, 1973; Hendrickson and Kingston, 1974).

Although we do not have sufficient data to determine the extent that fishes in CSM generally avoid or consume cercariae that can infect them

as second-intermediate hosts, we found 2 instances of fishes consuming cercariae that normally infect them through penetration (*C. ios* ate *S. hancocki*, and *L. armatus* ate *P. spindalis*; Table I). In some cases potential intermediate hosts, like the zebrafish, *Brachydanio rerio*, can reduce their risk of infection by consuming cercariae before the cercariae are able to penetrate their surface (Anderson et al., 1978).

Whether cercariae comprise an important part of fish diets in estuaries is unclear. Kuris et al. (2008) estimate that in aquatic habitats at CSM, infected snails produce 5 g/m<sup>2</sup> of cercariae annually, while the standing-stock biomass of fishes in these habitats is 10.3 g/m<sup>2</sup>. What proportion of the energetic needs of the fish community might cercariae meet? Perez-Espana et al. (1998) estimate that the California killifish population in the Ojo de Liebre estuary has an annual energetic need of 20.8 g crustacean/g of fish. Assuming the fish community in CSM has a similar per gram consumption rate as the killifish population at Ojo de Liebre, this would translate to >200 g of food consumed by fish/m<sup>2</sup>/yr in CSM. Assuming the energetic content of cercariae is comparable to crustaceans, and that fish eat most cercariae produced, suggests that cercariae produced in this system could supply up to 2–3% of the energetic needs of the fish community. If most cercariae consumed are eaten by juvenile fishes, then the proportion of their diet that cercariae comprise may be considerably greater than 2–3%. Although 2–3% is not a substantial figure for the entire fish community, cercariae might be an important resource at certain places and times, and it seemed logical to include trematode cercariae in aquatic food webs (Lafferty, Dobson, et al., 2006). Currently estimates are underway to determine the cercarial proportion of the CSM zooplankton community as well as their actual caloric value.

Predation is likely a common source of mortality for free-living stages of parasites, and most studies indicate predation can greatly reduce transmission (Thieltges et al., 2008). Whether predation by fishes is a significant source of mortality for cercariae in CSM remains an hypothesis. In aquaria fishes can consume all available cercariae, and, in the field, we estimate that the consumption of cercariae is significant enough to impact food-web dynamics. Invertebrate predators might also be important sources of mortality. Clams and polychaetes consume cercariae (Lafferty, Hechinger et al., 2006), and their biomass density is higher than that of fishes in estuaries such as CSM (Kuris et al., 2008). However, the nature of the predator and the effect of predation on the cercariae likely vary depending on the trematode species. Manipulating predator abundance and tracking changes in transmission of trematodes to second-intermediate hosts is the next logical step to evaluate this hypothesis. Predation on trematode cercariae could affect energy flow and transmission dynamics in this estuarine ecosystem, and it is likely that other ecosystems are similarly affected. Incorporating predation on



parasites into energetic and transmission models of aquatic ecosystems will improve our picture of transfer of energy and patterns of infectious diseases.

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