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Trematodes Indicate Animal Biodiversity in the Chilean Intertidal and Lake Tanganyika

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ABSTRACT: Trematode communities in populations of estuarine snails can reflect surrounding animal diversity, abundance, and trophic interactions. We know less about the potential for trematodes to serve as bioindicators in other habitats. Here, we reanalyze data from 2 published studies concerning trematodes, 1 in the Chilean rocky intertidal zone and the other from the East African rift lake, Lake Tanganyika. Our analyses indicate that trematodes are more common in protected areas and that in both habitats they are directly and positively related to surrounding host abundance. This further supports the notion that trematodes in first intermediate hosts can serve as bioindicators of the condition of free-living animal communities in diverse ecosystems.

Can parasitic worms serve as indicators of surrounding animal diversity, abundance, and trophic interactions? Some should, because of fundamental aspects of their biology. Unlike most other organisms, many parasites with multiple-host life cycles are predictably and directly linked to several types of invertebrate and vertebrate hosts. Additionally, at some steps in their life cycles, most of these parasites use predator-prey interactions to get from host to host. Thus, these parasites require both the presence of each of their hosts and a functioning food web (Gardner and Campbell, 1992; Marcogliese and Cone, 1998; Huspeni et al., 2005; Hudson et al., 2006). Among such parasites, trematode flatworms are particularly promising ecological indicators (Huspeni et al., 2005). Not only are trematodes associated with surrounding biodiversity and food webs, they are, importantly, easily sampled in their first intermediate hosts (Huspeni et al., 2005). Work supporting the development of larval trematodes as indicators has directly assessed the association of trematode communities in snail populations with surrounding free-living fauna (Smith, 2001; Hechinger and Lafferty, 2005; Lafferty and Dunham, 2005; Lafferty et al., 2005; Fredensborg et al., 2006; Hechinger et al., 2007; Whitney et al., 2007). For instance, trematode diversity and abundance can correlate with that of surrounding bird communities (Smith, 2001; Hechinger and Lafferty, 2005; Fredensborg et al., 2006; Whitney et al., 2007).

Research directly examining associations between trematodes in snails and surrounding free-living communities has primarily been based in estuaries. There are few, or no, data to evaluate the potential for trematodes to serve as indicators in nonestuarine habitats. However, trematodes are widespread, and their ability to act as indicators should not be restricted to estuaries (Huspeni et al., 2005). Here, we briefly consider 2 studies of trematodes and their hosts, 1 from the rocky intertidal in Chile (Loot et al., 2005) and another from a rift lake in East Africa (McIntyre et al., 2005). We analyze data from these studies to evaluate the promise of developing trematodes as indicators of the abundance of surrounding free-living animals and trophic interactions in these types of ecosystems.

In Chile, Loot et al. (2005) studied parasitism in 2 rocky intertidal reserves and 2 areas fully open to fishing. The trematode, Proctoeces lintoni, was more common in first intermediate host mussels and second intermediate host limpets in reserves compared to exploited areas. Loot et al. (2005) suspected that the reserves had higher levels of parasitism in these hosts because reserves harbored greater densities of final host fishes (which should increase the transmission of parasites to mussels). Yet, Loot et al. (2005) found no differences between reserves and exploited areas in their 2 measures of parasitism of fishes by adult worms (prevalence and mean abundance, sensu Bush et al., 1997). However, we used their data to measure parasites as both the density of infected fishes and the density of adult trematodes living in fishes. We calculated the density of infected fish by multiplying fish density by infection prevalence. Trematode density is the product of fish density and the mean number of trematodes per individual fish (mean abundance). We performed statistics on our derived measures with the use of standard errors obtained by applying general rules of error propagation (Taylor, 1982) to the standard errors and degrees of freedom provided in Loot et al. (2005). We used an analysis of variance allowing unequal variances (Rice and Gaines, 1989, 1993) to assess the significance of differences among all sites and a *t*-test allowing unequal variances (Norman and Streiner, 2000) to assess whether average densities (weighted by sample size) of infected fishes or trematodes differed at exploited sites compared to protected sites. These analyses show that reserves also harbored both greater densities of infected fish (Fig. 1a) and greater densities of adult trematodes (whose offspring infect mussels) (Fig. 1b). This further supports the idea (Hudson et al., 2006) that a "healthy" ecosystem is 1 that is rich in parasites.

Can measures of trematodes provide an assessment of the success of the rocky intertidal reserves in protecting biodiversity? Generally, for

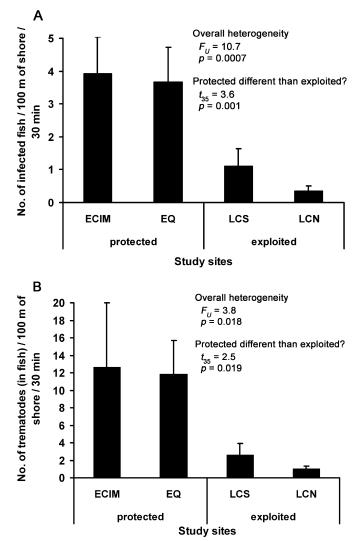


FIGURE 1. (a) Density of infected final host fish (\pm SE), and (b) density of trematodes living in final host fishes (\pm SE) at protected and exploited study sites in the rocky intertidal. These data are derived from data given in Loot et al. (2005, see text). The F_U statistic is from an analysis of variance allowing unequal variances examining whether there is overall heterogeneity across sites, and the *t*-test (allowing unequal variances) directly assesses whether protected sites differ from exploited sites (see text).

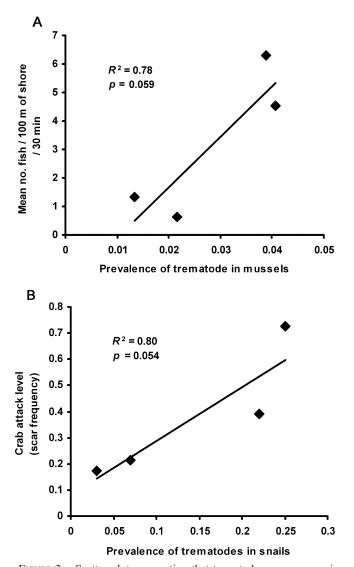


FIGURE 2. Scatter plots suggesting that trematodes can serve as indicators of (**a**) fish abundance and (**b**) crab abundance (for which crab attack rates on snails likely serve as a proxy). Data for (**a**) are replotted from Loot et al. (2005) and data for (**b**) are from McIntyre et al. (2005)—see text. The *P* values are 1-tailed. Fitted lines are ordinary least-squares regression lines. Taken together, both studies support the general hypothesis that trematodes indicate surrounding diversity, with a consensus *P* value of 0.012.

an indicator to be useful, it must be both easier to sample than the character of interest and tightly associated with it (McGeoch, 1998). In the Loot et al. (2005) study system, fish are more difficult to sample than mussels; therefore, using mussel parasites as indicators is appealing. We plotted the data, from Loot et al. (2005), of fish density versus trematode prevalence in mussels. Although there are only 4 data points, the data indicate that fish density is tightly related with trematode parasitism in mussels (Fig. 2a). This provides evidence that trematodes may serve as indicators for the effectiveness of rocky intertidal reserves in protecting fished species.

A study by McIntyre et al. (2005) on effects of disturbance on a snail assemblage in an East African rift lake (Lake Tanganyika) provides similar insights into the use of trematodes as indicators. Here, trematodes are less prevalent in snails at sites degraded by anthropogenic sedimentation. Do the disturbed sites harbor a lower abundance or diversity of surrounding animal life? Although McIntyre et al. (2005) did not present data on the rest of the community at their study sites, they provided data that serve as a proxy for crab abundance, i.e., they used

snail shell damage as an indicator of the intensity of interactions with predatory crabs. These crabs may serve as prey for vertebrate definitive hosts and also likely act as second intermediate hosts for some of the unidentified trematodes. Therefore, areas with more crabs (and a higher prevalence of crab attack marks on snail shells) may also have more trematodes in snails. To assess this relationship, we plotted data from McIntyre et al. (2005) on the prevalence of crab attacks versus the prevalence of trematode infection in snails. For the prevalence of crab attacks at each site, we calculated mean scar frequency across elevations (weighted by snail density). We used the prevalence of parasitism in adult-sized snails. Here too, we have only 4 data points, but the scatter plot indicates that these variables are tightly and positively correlated (Fig. 2b). A link between crab abundance and trematodes could result from increased life-cycle completion of trematodes that use crabs as second intermediate hosts. The relationship could also occur if an abundance of crabs attracts mammalian definitive hosts (otters prey upon crabs in this system; P. B. McIntyre, pers. comm.). In the latter case, trematodes in snails would also be good indicators for the abundance of otters.

Despite the small sample sizes, each of these studies provides at least marginally significant results that lie exactly in the direction predicted by the hypothesis that trematodes in first intermediate hosts are indicators of surrounding free-living diversity and trophic interactions. However, we can go further and statistically assess the overall support these 2 analyses give to the general hypothesis. This can be done by combining the *P* values of each test with the use of the *Z*-transform procedure (Strube and Miller, 1986; Rice, 1990). This method of combining *P* values is useful in examining the consensus of multiple independent statistical tests that examine the same general hypothesis, but the raw data of each study cannot be pooled, e.g., due to differences in methods (Rice, 1990). This mini-meta-analysis gives a significant result (*P* = 0.012), demonstrating the consensus of the 2 analyses, i.e., that trematodes are positive indicators of surrounding diversity and ecological interactions.

Our reanalysis of data from the studies of Loot et al. (2005) and McIntyre et al. (2005) simply highlights the potential of trematodes to serve as indicators of biodiversity and food-web function in widely differing ecosystems. We found significant results despite small sample sizes, indicating the associations are very strong. We hope this note spurs more in-depth examinations of trematodes as bioindicators in these and other systems. Promising trematode-host bioindicators are common throughout the world in many types of aquatic and marine habitats (Huspeni et al., 2005). Most importantly, in many cases, a speciose guild of trematodes uses the same species of first intermediate host snail. Such guilds capture much of the complexity of the surrounding community because the different trematode species use different second intermediate and final hosts. These parasites are very easily sampled compared to surveying entire communities of invertebrates, fishes, birds, or mammals. This suggests that trematodes in first intermediate hosts can provide cost-effective and useful information regarding the surrounding ecosystem. In a time when the importance of biodiversity monitoring is escalating (e.g., Noss, 1990; Dobson, 2005), the widespread use of trematodes as bioindicators should be seriously considered.

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