Environmental Parasitology:
What can Parasites tell us about Human Impacts on the Environment?

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There are a variety of ways that environmental changes affect parasites, suggesting that information on parasites can indicate anthropogenic impacts. Parasitism may increase if the impact reduces host resistance or increases the density of intermediate or definitive hosts. Parasitism may decrease if definitive or intermediate host density declines or parasites suffer higher mortality directly (eg. from toxic effects on parasites) or indirectly (infected hosts suffer differentially high mortality). Although these scenarios are opposing, they can provide a rich set of predictions once we understand the true associations between each parasite and impact. In this review, Kevin Lafferty discusses how parasite ecologists have used and can use parasites to assess environmental quality.

There has been a growing number of reasonably successful attempts to use parasites in environmental impact studies[1-6]. The vast majority of these investigations have focused on the effects of pollution (eutrophication, pulp-mill effluent, thermal effluent, oil, acid precipitation, sewage and heavy metals) on the parasites of fishes[6] (mostly ciliates, nematodes, monogenes, cestodes, acanthocephalans and digenes), and, to a lesser degree, larval digenes in gastropods. Many studies have also examined the relationship between generalized human 'disturbance' (usually concerning the effects of humans and development on bird abundance) and larval digenes in gastropods[7]. Comparisons in terrestrial systems are relatively uncommon but include studies of insects[8-10], and helminths of primates[11] and marsupials[12].

Environmental assessment

Most environmental assessments involve quantifying a measure chosen to reflect impacts caused by pollution or other disturbances. Different measurements have various advantages and disadvantages.

* Physical measurements, such as the concentration of a pollutant, can often provide precise and unambiguous quantification of potentially harmful substances. However, physical measurements do not indicate ecological impacts and, contrary to frequent assertions, are not less expensive than biological monitoring[13].
* Bioassays (eg. on the easily cultured mosquito fish), which test the effects of water or soil from the impacted region, can provide an inexpensive standardized assessment of toxicity. Siddall and Des Clers[14] provide a good example of the mostly untapped potential for using digene cercariae and miracidia as bioassays. Another approach is to expose hosts to substances in the laboratory and compare the survivorship of parasites[15] or infected hosts[16] between treatments and controls. A drawback of bioassays is the limited extent to which they can predict effects on the community at large. This is because bioassays test a laboratory animal over a short time, and may not evaluate sublethal effects[17].
* Organisms that tolerate and accumulate toxins can act as 'sentinel species' for mapping the distribution of a pollutant[18]. Sentinel species need to be ubiquitous, sedentary and long-lived. Because sentinel species are tolerant, they do not yield much information on impacts to other species in the environment. It seems unlikely that parasites will make good sentinel species, although their hosts certainly may.
* Measurement of the abundance of 'indicator species' – organisms known to be sensitive to or associated with a particular impact (eg. some benthic annelids[19]) – reflects the actual impacts to the environment better than do the previously described measures. The typical use of parasites in environmental assessments is as indicator species. The most common approach is to compare the prevalence or intensity of parasitism among hosts captured from a small number of control and impact sites[20] or a single site before and after an impact[21,22]. It is also possible (but less common) to quantify parasitism at varying distances from a point source or along a gradient of an impact[13,23].
* In some cases, 'species of special interest' (such as endangered species or species that play a key role in community organization) make justifiable environmental indicators. Parasites of medical or veterinary concern, or those that regulate host populations, particularly pests, might be of special interest.
* 'Species diversity' [usually limited to the measurement of a taxonomic group (eg. fishes) or functional guild (eg. benthic infauna)] gives a more comprehensive view of the community in question but can be costly to assess (Box 1). Unfortunately, it is not always clear how diversity should vary with particular impacts (because some species may increase while others decline).
* The grouping of several indicator species to form 'biotic indices' (eg. ratios of meiofaunal nematodes to copepods[24]) provides a broader reflection of impacts[25]. The use of biotic indices requires a firm understanding of the associations between the indicator species and the impact of interest. Also, biotic indices usually reflect only a specific type of impact[26].
* The most comprehensive approach is to combine multiple measurements into a single index. An 'index of biological integrity' can be built from a

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series of measures of an assemblage (in freshwater systems, these assemblages are typically fishes, invertebrates or diatoms) that encompass species richness and composition (distinguishing between tolerant and intolerant species), trophic composition (percentage herbivores, omnivores and predators), condition (percentage diseased, percentage abnormal) and abundance (see Ref. 26 for a review). Hopefully, we will see attempts to incorporate parasites into indices of biological diversity in the future.

Analysis of the evidence

The various means by which parasites might respond to environmental change make predictions difficult. Not surprisingly, previous reviews have bemoaned the conflicting nature of the evidence. I was curious to see if some patterns would emerge from

the wide range of results. I followed Poulin's approach[5], recording for available studies the host, parasite, environmental factor of interest, and the direction of effect on parasite numbers (based on the authors' interpretations). Some studies provided more than one comparison, resulting in a total of 163 comparisons. Although space constraints prohibit referencing each comparison, most are cited within the references of this article (eg. Refs 1–6).

To investigate associations between parasites and environmental degradation, I calculated a standardized effect, E, by granting comparisons showing an increase in parasites (a positive effect), no effect on parasites (a neutral effect) and a decrease in parasites (a negative effect) scores of 1, 0 and −1, respectively, and then taking the mean. Overall, the association between parasites and environmental degradation was weak. This is because environmental factors differed in their effects and parasites differed in their responses (Table 1). For example, eutrophication increased parasitism, while heavy metals and unspecified human 'disturbance' reduced parasitism. Also, ciliates responded positively to impacts, while digenes responded negatively. The other parasites were less consistent in their response, due, in part, to the range of effects that different types of impacts had on parasites. The diversity of pollutants and parasite groups placed within 'industrial effluent' and 'other groups', respectively, probably led to the conflicting directional effects that resulted in low net values of E.

Because of these inconsistencies, predictions need to match specifically the sensitivities of the parasites and the effect of the perturbation. The potential for environmental factors to increase some parasite groups and decrease others suggests that Table 1 is a relatively inefficient way to make predictions. Parceling out the effects in two dimensions helps clarify the predictions substantially (Table 2). For example, although there appears to be no net effect of crude oil on parasites ($E = +0.08$), this is because crude oil has opposing effects on different parasite groups. In Table 2, the clearest predictions occur in the upper left and lower right corners of the matrix: ciliates and nematodes should be sensitive indicators of eutrophication and thermal effluent, while digenes and acanthocephalans should make good indicators of heavy metals and human 'disturbance'. These predictions are reasonably consistent with the results from the literature. The center, lower left and upper right corners are more difficult to predict. Although I found no studies of

Table I. Associations between environmental impacts and parasites

	Effect				
	Positive	Neutral	Negative	E^a	P^a
Impact[b]					
Heavy metals	2	0	13	−0.73	<0.05
'Disturbance'	3	0	15	−0.67	<0.05
Acid precipitation	1	2	3	−0.33	NS
Sewage-sludge	3	7	6	−0.19	NS
Industrial effluent	15	6	22	−0.16	NS
Crude oil	6	1	5	+0.08	NS
Pulp-mill effluent	14	3	9	+0.19	NS
Thermal effluent	9	1	5	+0.27	NS
Eutrophication	11	0	1	+0.83	<0.05
Parasite group					
Digenea	13	1	31	−0.40	<0.05
Acanthocephala	5	2	11	−0.33	NS
Cestoda	6	4	11	−0.24	NS
Other groups	10	6	13	−0.10	NS
Monogenea	12	5	9	+0.12	NS
Nematoda	7	2	4	+0.23	NS
Ciliophora	11	0	0	+1.00	<0.05
Total	**64**	**20**	**79**	**−0.09**	**NS**

[a] E represents the mean effect (by granting positive, neutral and negative comparisons scores of 1, 0 and −1, and then taking the mean). P is based on the two-tailed sign test with Bonferroni correction. Comparisons were drawn from the literature.
[b] The first list organizes comparisons by impact; the second list organizes comparisons by parasite group.

Table 2. A matrix of the most frequently studied parasites and types of pollution (derived from Table 1)[a]

Parasite	Eutroph-ication	Thermal effluent	Pulp-mill effluent	Crude oil	Industrial effluent	Sewage-sludge	Acid precipitation	Disturbance	Heavy metals
Ciliophora	n	+	+	+	+	n	n	n	n
Nematoda	+	+	+/−	+	−/+	=	n	+/−	n
Monogenea	+	+/−	−/+	+	+/−	=	−	−	n
Other groups	+	+/−	+	−	−	=	=	−	+
Cestoda	+	=	n	n	−/+	+	−	−	−
Acanthocephala	+	+/−	n	−	−	−	+	n	−
Digenea	+	−	−/+	−	−/+	−/+	−	−	−

[a] The symbols represent the direction of the effect (E) based on single comparisons (+, positive; =, neutral; −, negative), multiple inconsistent comparisons with a positive (+/−) or negative (−/+) bias, or multiple, yet consistent comparisons (bold +, −, or =). The letter n represents a comparison for which I could not find an example.

ciliates and heavy metals (except for the use of metals as therapeutic agents in aquaculture), the data for digenes suggest that they can increase with eutrophication.

Where to go from here

There are several ways that we can use parasites to assess environmental impacts. First, certain free-living stages of parasites could serve as bioassays for water quality. Digenes, in particular, have the advantage that a single genome can supply replicate tests because germ sacs in snails produce many cercariae asexually. For example, sewage-sludge reduced survival of cercariae and miracidia, leading to a lower prevalence of *Zoogonoides viviparous* in snails[14], despite high host abundance[27]. Second, the presence of parasites on/in hosts (eg. ciliates on fishes, Box 2) may indicate physiological stresses suffered by hosts. Third, some parasites might prove to be good indicator species if their abundance correlates consistently and logically with certain impacts. For example, quantifying the presence or absence of digenes in fishes may be an efficient way to measure impacts of acidification in watersheds because acidification reduces populations of intermediate host snails (Box 1). Likewise, the diversity and prevalence of larval digenes in snails provide potentially useful indicators of disturbances that reduce the abundance and diversity of vertebrates (especially birds) that act as the digenes' final hosts[7] (Box 3).

The complexity of Tables 1 and 2 suggests that it may be unprofitable to use single measures of communities of parasites (such as species richness) as indicators of specific environmental changes because different taxonomic groups can respond in opposite directions. However, community-level monitoring will provide a detailed assessment of environmental change as long as analyses take into account the relative sensitivities of each group. This approach requires a better understanding of the associations between the wide range of parasites and impacts. Table 2 generates a number of

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Box 2. Ciliates on Fishes as Indicators of Host Stress

Trichodinid gill ciliates of fishes appear to be the parasite most consistently associated with water pollution. The aquaculture and aquarium industries are well aware that stressed fishes in crowded tanks with poor water quality are highly susceptible to gill parasites[28]. Intensities or prevalences of ciliates increase with oil pollution[29], pulp-mill effluent[30–32], industrial effluent[33–35] and thermal effluent[36,37]. The increase in ciliates appears to be due to an increased susceptibility of fishes, because toxic conditions compromise their immune systems[29]. Findings that ciliate intensities can be coincident with other forms of pathology such as decreased lymphocyte levels, hyperplasia in the gills, increased diameter of gill lamellae[15], and liver anomalies[31] support this supposition. The pathology that seems most directly associated with ciliates is a toxicant's ability to impair mucus production, a fish's chief defense against gill parasites[38].

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clear predictions for specific impacts that could be suitable for creating biotic indices. For example, the ratio of ciliates to digenes of fishes should provide a powerful biotic index of the effects of crude oil. Eventually, these sorts of data could provide habitat-specific indices of biological integrity similar to those that now use free-living species exclusively.

Most measurements obtained in the laboratory suffer from the limitations discussed above. Many of the field studies, though more relevant, base their conclusions on inadequately replicated designs. Unfortunately, studies that combine field and laboratory

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Box 3. Larval Digenes in Snails as Indicators of Disturbance

Changes in the environment may affect larval digenes at many stages of their complex life cycles. My interest in this topic was first stimulated by observing a small urban population of the horn snail *Cerithidea californica* separated from a marsh by a parking lot and bordered by a busy highway intersection: birds were conspicuously absent and the snails were completely uninfected compared with a prevalence of infection of 25% in the adjacent marsh[39], suggesting that disturbance reduced digene prevalence. Other authors have also speculated that the prevalence of digenes corresponds to the degree of habitat degradation[40–43]. Cort *et al.*[44] were the first to investigate such an association. They found that larval digene diversity and species richness had declined since studies 20 years previously. They also noted an increase in human disturbance and a reduction in the shore-bird population. Keas and Blankespoor[22] recently resampled these sites and found continued declines. However, some species, presumably those that parasitize birds associated with humans, had increased. A case of the latter is a sharp increase in swimmer's itch in Moscow associated with pollution and human disturbance[45]. Here, eutrophication has improved conditions for snails. Added to this is a thriving population of urban-adapted mallards (escaped from local farms), fueling the life cycle of *Trichobilharzia ocellata*. These examples underscore the need to improve our understanding of the life cycle of each digene species, distinguishing species harmed by disturbance from those that benefit from it.

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evidence[31] are rare. Also, host vagility may obscure the impacts of pollution because parasites may not reflect conditions at the site of collection[38], emphasizing the value of sedentary host species. There are so many factors that can cause spatial and temporal variability in parasite populations that it is tenuous, at best, to assign such differences to a single factor – if, as in most field studies, the comparison is only before and after an impact, or between a single impacted site and a single reference site[46,47].

Fortunately, there are now a number of sampling designs that help to overcome confounding spatial and temporal variation in the environment. 'Before-after-control-impact' (BACI) designs are useful in that they can accommodate spatial and temporal heterogeneity[48]. They are most appropriate for cases where we foresee an impact and can acquire adequate baseline information at sites that will and will not experience the impact. Temporal[49] and spatial[50] replication can substantially improve BACI designs because statistical tests require independent, interspersed replication. If it is not possible to obtain information on a site before an impact, 'matched pairs' designs may be useful. These designs use several impact sites, each with appropriate reference sites. BACI and matched pairs designs are best for distinct qualitative impacts such as might follow an oil spill.

'Gradient designs' are appropriate when the strength of the impact varies in space (eg. the diffusion of a pollutant away from a point source). Here, sampling occurs along an exposure gradient, and can provide regression models for predicting the magnitude of future impacts. For example, Siddall et al.[51] showed that the presence of larval digenes in snails decreases as a function of the distance from a sewage-sludge dump site. As with any correlational analysis, interpretation may suffer from unknown covariates. For instance, Curtis[52] found that digenes decreased with pollution, yet inverse associations of each variable with depth confounded this association.

Time series data can help determine if impacted sites recover. Briefly, 'impact level-by-time' studies compare how an indicator changes over time at an impacted and reference site(s). The site has supposedly recovered when the impact and reference trajectories converge with time. 'Impact trend-by-time' studies are similar to impact level-by-time studies. For these comparisons, one regresses measurements of an indicator against a gradient of the impact at repeated time intervals. The impact is no longer significant when the slope of the association is zero.

In conclusion, despite the impressive amount of existing information, there are still a number of important gaps in our knowledge. Only in a few of the parasite–pollutant combinations in Table 2 is there enough information to make a strong and general prediction. Furthermore, several combinations have gone entirely unexplored. We also need more information on hosts other than fishes and on the mechanisms responsible for the observed associations between parasites and impacts. Perhaps the most important step will be to adopt better study designs widely used in environmental impact assessment. With these improvements, environmental parasitology will contribute substantially to future impact assessments.

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The Epidemiology and Control of Cattle Schistosomiasis

J. De Bont and J. Vercruysse

Schistosomiasis remains a major health problem in much of the developing world. Despite decades of research, many fundamental questions on the dynamics of infection and immunity development remain unanswered. Schistosomiasis is also a common parasitic infection in cattle, and studies on livestock exposed to their own species of schistosome may help in understanding some aspects of the host–parasite relationship. Here, Jan De Bont and Jozef Vercruysse review the current knowledge on the epidemiology and control of cattle schistosomiasis.

Schistosomiasis is a major medical problem in many tropical and sub-tropical regions. Over 200 million people are believed to be affected worldwide and effective long-term control has proved difficult. As a result, research has been conducted in a wide range of disciplines aimed at understanding and alleviating schistosome infection[1,2]. The epidemiology of human schistosomiasis in the field has received particular attention. Egg counts in excreta and, in recent years,

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antigen-detection assays[3] and ultrasonography[4] have been the main techniques used to measure intensity and morbidity of infection. However, many fundamental questions on the dynamics of infection and host immunity remain unanswered[5]. A major factor restricting epidemiological studies of human infection is that it is not possible to count worms *ante-mortem* in infected subjects.

Schistosome infections also occur in cattle but, except for occasional reports of field outbreaks[6-10], there has been little recognition of their veterinary significance. The clinical and pathological aspects of acute schistosomiasis have been examined in detail, together with the evolution of the host–parasite relationship and development of immunity in cattle[10,11]. Most studies have been based on experimental infections, with only a small number of field epidemiological reports. This is surprising because infections in cattle are widely distributed and occur commonly throughout Africa and Asia. It has been argued that, in the long term, such infections cause significant losses to farms[12]. In addition, cattle present unique advantages for field studies aimed at improving our understanding of the epidemiology of schistosomiasis. They are the natural definitive hosts of at least ten