

HOST PARASITE INTERACTIONS AND INFECTION PATTERNS OF HELMINTHS IN CATLA CATLA FROM THE INDUS RIVER AN ECOLOGICAL AND PUBLIC-HEALTH PERSPECTIVE

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Abstract

*Helminth parasites are a part of the freshwater ecosystems and have an estimateable effect on the health, productivity, and economic value of fish populations. A major food fish of the Indus River system in Pakistan, catla catla (Hamilton, 1822) is one of the most commercially significant species of major Indian carps, yet, its host-parasite interactions have been poorly studied in this region. The current article re-analyzes the results of a survey of 26 Catla taken in the Indus River at Jamshoro, Sindh, during January 2018-January 2020 and interprets the resulting patterns of infections as an ecological and public-health phenomenon. The percentage of hosts that harbored helminths was nine out of 26 (34.6%) and six taxa were identified: trematodes (*Thaparotrema pedicellatum*, *Isoparorchis trisimilitubis*, *Echinochasmus* sp.), nematodes (*Procamallanus (Spirocamallanus)* sp., *Rhabdochona* sp.). The overall prevalence was led by trematodes (23.07%), with nematodes showing the most common mean intensity (14 worms per infected host). Parasites were categorically divided into four microhabitats, i.e., gall bladder, body cavity/swim-bladder, intestine, and stomach, where 52% of all worms observed were recovered in the intestine. The patterns of infections agreed with the ecology of the host surface/midwater feeding and the availability of the intermediate host locally and the existence of the piscivorous birds along the river. The rediscovery of *Echinochasmus* has direct food-safety consequences, with several species of the genus being food-borne zoonoses that are carried in undercooked fish flesh. The results emphasize the importance of systematic parasite surveillance of the Indus fishery and provide identified interventions to the fisheries management and consumer protection.*

1. Introduction

The presence of parasites is one of the ubiquitous characteristics of aquatic communities. They are present in all freshwater bodies that have been sufficiently surveyed and they influence host populations by influencing growth, reproduction, behaviour and survival. Helminth infection can impair organ functions in fish, lower condition factor, decrease fecundity, and, in extreme situations, lead to death [1]. The economic implications are high: in some countries, like Pakistan, where inland fisheries are the source of livelihood of millions of people, and the presence of moderate parasite loads can be converted into quantifiable losses on both producer and consumer sides.

Catla catla (Hamilton, 1822) is one of the most suitable species of Indian carp among the most economical in South Asia [5]. It is a surface- and midwater-feeding cyprinid with juveniles feeding on phytoplankton and zooplankton, and adults on zooplankton. This predatory location puts the species at risk of a large variety of life cycles of parasites which have either copepod, snail, or oligochaete intermediate hosts. Despite the research on the parasites of *Catla catla* in India and Bangladesh [6, 7, 19, 22-29], the research on similar parasites in the Indus River, the main river system of Pakistan, has been rather minimal with only some previous records of acanthocephalans in Haleji and Kalri lakes.

The current article goes beyond the descriptive assignment of listing taxa and goes to the ecology of infection in *Catla catla*. It reuses the sample of 26 hosts studied at Jamshoro, Sindh, in 2018-2020 and poses four questions that are related to each other: (i) at what is the general and group-specific level of infection within the host population? (ii) what is the distribution of parasites amongst microhabitats in the fish? (iii) which transmission pathways are most likely to be implicated, in the biology of the identified parasites and the ecosystem around the area? and (iv) what do these patterns imply to fisheries management and food safety in the lower Indus? It is hoped that an ecological framework into which molecular and pathological work of the future can be integrated will be available.

2. Study System

2.1 The Indus River at Jamshoro

The Pakistan Indus River is the longest river of Pakistan, that is formed in the Tibetan Plateau and runs through Ladakh, Gilgit-Baltistan, Punjab, and Khyber Pakhtunkhwa and passes through the whole province of Sindh and empties in the Arabian Sea, through a large deltaic system. It has a series of six large barrages built along its bed, one of which (Kotri Barrage) at Jamshoro delimits the current area of study. The Kotri stretch is a combination of slow-moving reaches, riparian vegetation, off takes of irrigation and rich invertebrate communities, which are all conducive to the continuation of complex parasite life cycles. Dominating in the local fauna is the cyprinids (*catla catla*, *Labeo rohita*, and *Cirrhinus mrigala*) and bagrid catfishes (*Rita rita*, *Sperata sarwari*) [29]. Piscivorous birds, such as the little cormorant of which comprehensive helminthological research has been carried on in the same district [2] are not strangers to the river, and probably represent ultimate hosts to most of the trematode life cycles described here.

2.2 The Host Species

Catla catla can be identified by features of its large broad head, upward facing mouth, large greyish scales on the body except the belly which is whitish and high rate of growth; given favourable conditions it grows up to 182 cm long and 38.6 kg in weight [5]. Notably in parasitology, juveniles feed on phytoplankton and zooplankton and adults feed on zooplankton. Such a dietary profile forecasts a community of parasites as assembling predominantly by trophic transmission via copepoda and zooplanktonic intermediate hosts. The species is taken in large quantities at Jamshoro, and is a part of the daily food of the neighboring human population, rendering its parasites of interest both to fisheries and to the public-health.

2.3 Sampling and Examination

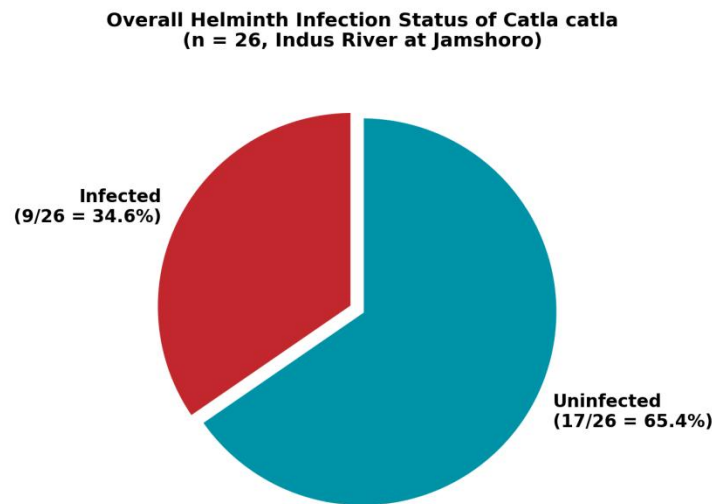
Between January 2018 and January 2020, twenty-six adults *Catla catla* were caught at several landing locations within the Kotri reach, either directly purchased out of the hands of the local fishermen or through assisted netting (cast and basket nets). Hosts were taken to Parasitology Laboratory of the Department of Zoology, University of Sindh, and each specimen was dissected using longitudinal

ventral incision. The visceral organs, gall bladder, swim-bladder, body cavity, oesophagus, stomach, and intestine were put in physiological saline and studied one at a time under a stereomicroscope. The recovered helminths were treated according to Schmidt [30] and Garcia and Ash [31]: the trematodes and acanthocephalans were stained in borax carmine, and placed in Canada balsam, whereas the nematodes were examined in temporary glycerine preparations. A standard taxonomic key of Yamaguti [32-34] and Soulsby [35] was used to identify the unknown organism.

3. Patterns of Infection

3.1 Overall Prevalence

Among the 26 *Catla catla* sampled, 9 individuals (34.6%), were found to harbour at least one helminth taxon (Figure 1; Table 1). Despite a moderate sample, this general prevalence is similar to those of the *catla catla* in West Bengal [19] and Andhra Pradesh [6], and indicates that the helminth load of the Indus population at Jamshoro is generally typical of the species in South Asia.



*Figure 1. Overall infection status of the 26 *Catla catla* hosts examined. Nine of the 26 (34.6%) were infected with at least one helminth taxon.*

3.2 Parameters of Infection by Helminth Group

The parameters of infection in the three recovered helminth groups differed significantly (Table 1; Figure 2). The most common group was trematodes, which had 6 out of 26 hosts (23.07%), but their average intensity of infection was comparatively small - about 4.7 worms per infected host. Only 2 hosts were infected (7.69%), but with relatively heavy infections with an average of 14

worms per infected host (primarily due to *Rhabdochona* sp., which produced 21 specimens per host). Only one host (3.84% prevalence; 7 worms in that host) yielded acanthocephalans (*Dispirin* sp.). The differences in the profiles, between trematodes and nematodes, which are distributed among many and few hosts respectively, are indicative of various transmission ecologies, as explained in Section 4.

Table 1: *Infection parameters of helminth groups in *Catla catla* from the Indus River at Jamshoro (n = 26).*

Group	Hosts infected	Prevalence (%)	Worms recovered	Mean intensity*
Trematoda	6 / 26	23.07	28	4.7
Nematoda	2 / 26	7.69	28	14.0
Acanthocephala	1 / 26	3.84	7	7.0

Group	Hosts infected	Prevalence (%)	Worms recovered	Mean intensity*
Total	9 / 26	34.62	63	7.0

* Mean intensity = total worms recovered / number of infected hosts.

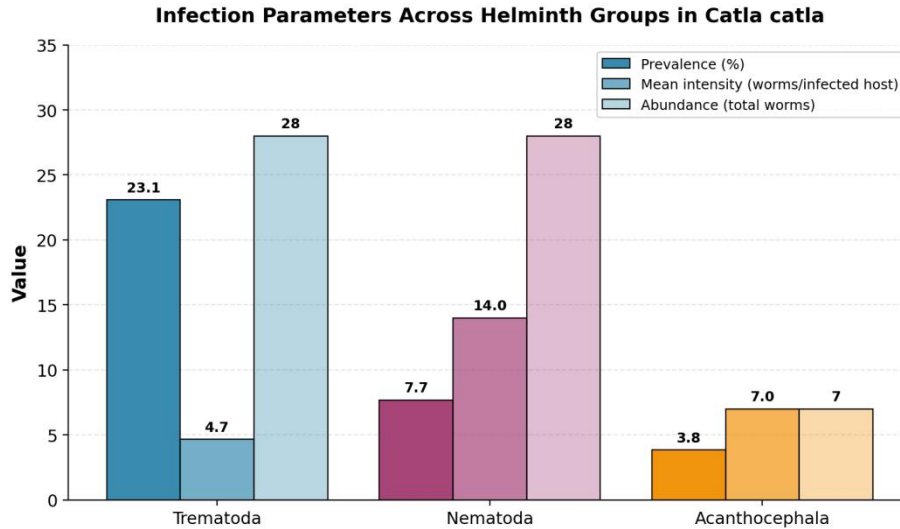


Figure 2. Prevalence (%), mean intensity (worms per infected host), and total abundance (worms recovered) for the three helminth groups in Catla catla.

4. Organ-Level Distribution and Microhabitat Partitioning

4.1 Where the Worms Are

The recovered helminths were not randomly distributed in the host during this study. Rather, they exhibited distinct microhabitat partitioning among four different organ systems: gall bladder, body cavity/swim-bladder, intestine and stomach

(Figure 3; Table 2). The most parasitized organ was the intestine, which harbored 33 of the 63 worms (52.4%), then the stomach (14 worms; 22.2%), then the body cavity/swim-bladder (9 worms; 14.3%) then the gall bladder (7 worms; 11.1%). All taxa of parasites had a single, typical microhabitat - no taxa overlap between organs (Figure 4).

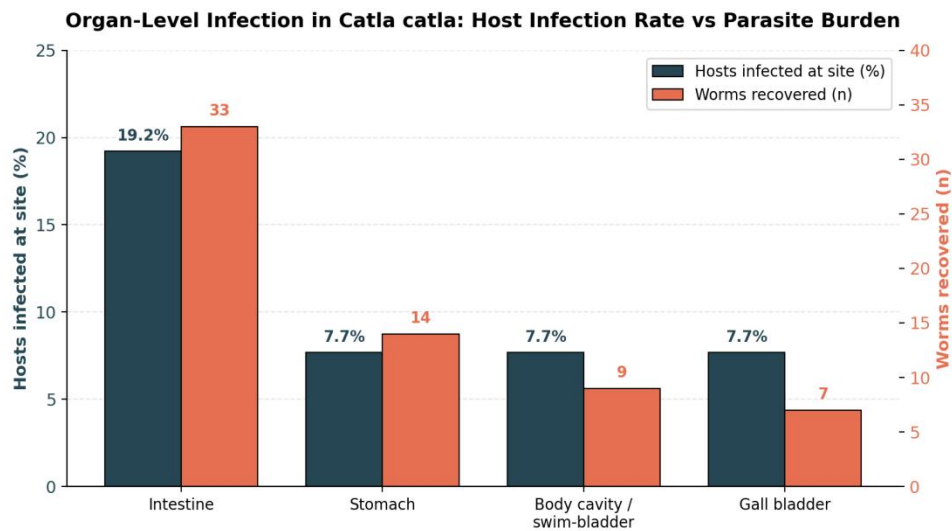


Figure 3. Organ-level infection in Catla catla. The dark-coloured bars (left axis) show the percentage of hosts infected at each site; the orange bars (right axis) show the total number of worms recovered.

Table 2: Microhabitat occupancy and parasite-organ associations in *Catla catla*.

Site of infection	Parasite taxon	Group	Hosts (n)	Worms
Gall bladder	<i>Thaparotrema pedicellatum</i>	Trematoda	2	7
Body cavity / swim-bladder	<i>Isoparorchis trisimilitubis</i>	Trematoda	2	9
Intestine	<i>Echinochasmus sp.</i>	Trematoda	3	12
Intestine	<i>Rhabdochona sp.</i>	Nematoda	2	21
Stomach	<i>Procamallanus (Spirocamallanus) sp.</i>	Nematoda	1	7
Stomach	<i>Dispirin sp.</i>	Acanthocephala	1	7

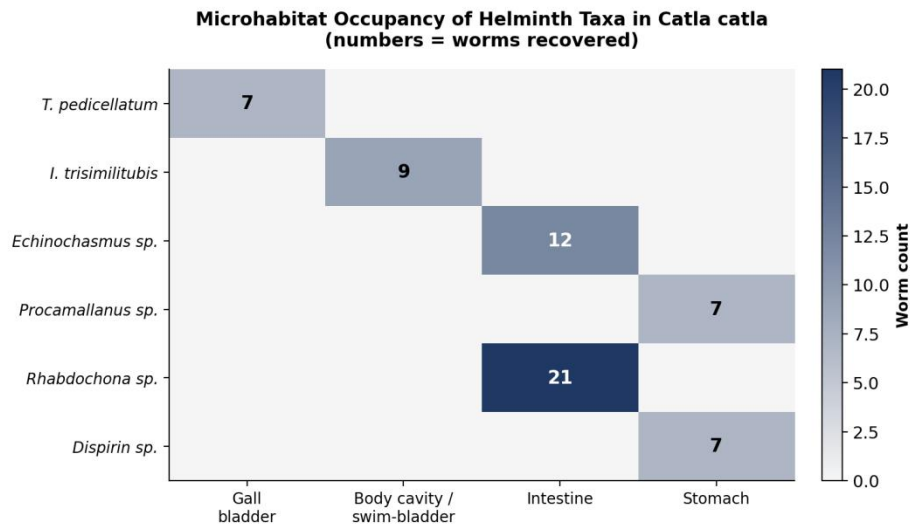


Figure 4. Heatmap of microhabitat occupancy showing the strict partitioning of helminth taxa among organ systems within *Catla catla*.

4.2 Ecological Interpretation of Microhabitat Partitioning

It is not that likely that the fact that no two helminth taxa were recovered in the same organ in this study was merely by coincidence. Microhabitat specialization is a documented characteristic of fish helminth communities and is an expression of physiological, behavioural and evolutionary processes. The data in this paper can be explained in three ways that are complementary.

First, there are significant physiological limits between organ systems. The chemically hostile and bile-ridden environment of the gall bladder is predisposed to the endospore like *Thaparotrema pedicellatum*, whose tegument and reproductive system are adapted to the presence of bile salts and the limited amount of fluid that

is present in the organ. The intestine by contrast provides a more constant source of food and a more moderate pH, and both *Echinochasmus* (a digenean that attaches to mucosal villi) and *Rhabdochona* (a nematoid that attaches to its toothed buccal cavity) can be found there. *Procamallanus (Spirocamallanus) sp.* and the acanthocephalan *Dispirin sp.* inhabit the stomach environment, where they feed on the food by their robust mechanical attachment structures (a sclerotized buccal capsule and a hooked proboscis, respectively), adapted to their microhabitat.

Second, transmission ecology directs various parasites in various organs. Those worms that have encysted infective stages in zooplanktonic intermediate hosts (e.g. *Procamallanus* in cope pods, *Rhabdochona* in mayfly larvae and ostracods) are digested in the foregut and

either stay in the foregut (stomach dwellers) or proceed downstream (intestinal dwellers) according to the activation cues they Trematodes like *Echinochasmus* enter have been shown to be metacercariae through second intermediate hosts, and excyst in the small intestine, with *Isoparorchis* [usually siluriform fishes [43-45] carrying out the role of a body-cavity host, but perhaps not the natural definitive host.

Third, competitive exclusion is a likely fine-tuning of the site occupancy. Niche partitioning minimizes direct competition even in cases where two taxa could coexist with the same organ in physiological aspects.

Echinochasmus and *Rhabdochona* were found in the intestine of a variety of hosts but not in one host in the present sample, indicating consistency with, but not, on this small sample, conclusive evidence of, competitive avoidance.

5. Transmission Pathways and Life Cycles

To comprehend the acquisition of the helminth fauna by catla, it is necessary to explicitly consider the life cycles of taxa. The recovered six taxa all have indirect (heteroxenous) life cycles that need at least one intermediate host. The overallized life cycle scheme, which arises out of the current data, is as follows in Figure 5.

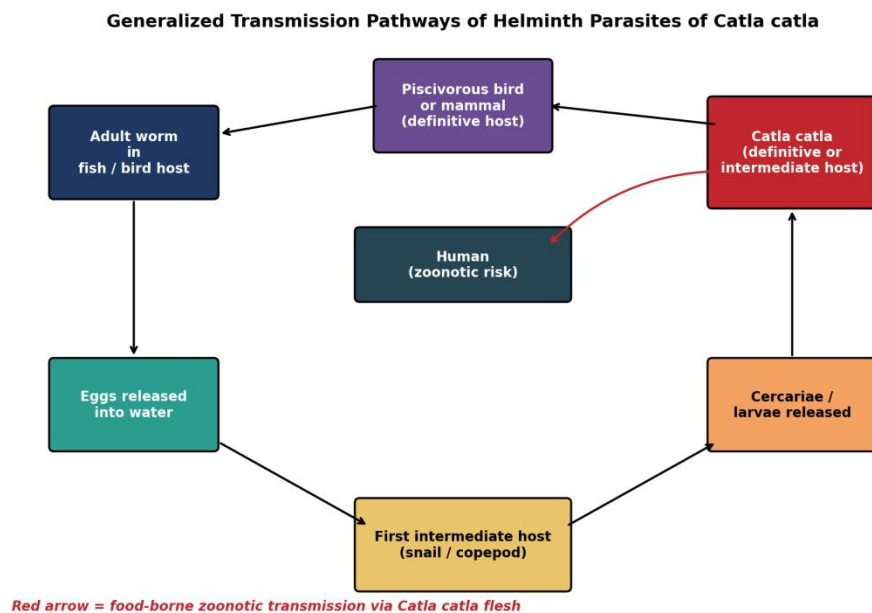


Figure 5. Generalized transmission pathways of helminth parasites of *Catla catla*. The red arrow highlights food-borne zoonotic transmission to humans through undercooked fish flesh – a route particularly relevant for *Echinochasmus* species [46].

5.1 The Trematode Pathway

The recovered trematodes are all digeneans whose life cycle is two-host or three-host. Typically, *Thaparotrema pedicellatum* (Opisthorchiidae) and *Echinochasmus* (Echinostomatidae) use freshwater snails as first intermediate hosts: cercaria released by snails cyst in fish (or, in some cases, in second intermediate hosts) and hatch to adults when the infected fish is eaten by a suitable definitive host. *Echinochasmus* species, especially, are generally familiar with their fish-bird and fish-mammal stages of life, and the infections obtained

here of *Catla catla* are likely to be metacercarial infections that have become adult worms due to host specificity plasticity, or - alternatively - are those acquired by fish prey through a piscivorous intermediate. *Isoparorchidae*: *Isoparorchis trisimilitubis* is unusual in that it inhabits the body cavity and swim-bladder of its fish host; its life-cycle includes a copepod first intermediate host and (normally) a siluriform fish as the definitive host [43-45], thus the current record of a cyprinid host is ecologically significant.

5.2 The Nematode Pathway

The life cycles of the two genera of nematodes here identified have well-defined small invertebrate first intermediate hosts. The species of the genus *Procamallanus* (*Spirocamallanus*) [47-50] have copepods as their intermediate hosts, and the catla catla - a zooplankton feeder - is a likely host of the parasite as a result of eating parasite-carrying copepods. This trophic transmission route is consistent with the recovery of seven worms (mature males and females) in one host. The rhabdochona species [51-58] are generally spread by mayfly nymphs, ostracods or amphipods, all of which are common in the sluggish water of Kotri Barrage. The extremely elongated intensity in a single host (21 worms) indicates that there was a recent feeding event on a highly infected invertebrate or a long-term ingestion of low-grade infections over an extended period.

5.3 The Acanthocephalan Pathway

Fishes are the typical intermediate hosts of acanthocephalans, and ostracods, amphipods or other small crustaceans are the typical intermediate hosts. The first record of the genus in this host, and in Pakistan, is *Dispirin* sp. found in the stomach of one *Catla catla*, and its complete life-cycle in the Indus system is yet to be clarified. By analogy with related genera, it has been inferred that the life cycle includes a benthic crustacean intermediate host that is accidentally ingested by *Catla catla* - perhaps in near-bottom foraging on demersal zooplankton or by accident when ingesting detrital particles. The hook-bearing, strongly muscular proboscis of the worm concurs with attachment to the gastric mucosa and the worm is associated with the gastric microhabitat of *Catla catla*, supporting both acanthocephalan and nematode parasites, although they were not found together in the same host in the present sample.

5.4 The Bird Connection

Trematodes like *Echinochasmus* and *Thaparotrema pedicellatum* are strongly suggestive of a role of piscivorous bird definitive hosts in the local transmission cycle of catla catla. The herons, cormorants, and kingfishers are typical of the Indus, and have been parasitologically studied in the same Jamshoro district [2]. The cycle is completed through birds that eat infected *Catla*

catla and lay helminth eggs in the river through their faeces. Any programme of management directed to the suppression of transmission must consequently not regard only the fish, but also the avian and invertebrate chain-links of the chain- a point of view at which pure descriptive parasitology can all too readily look.

6. Impact on the Host and Wider Implications

6.1 Effects on *Catla catla* Itself

Even though the current study lacked histopathological analysis, the identity, intensity, and microhabitat of the parasites recovered provide several valid inferences in relation to the impact of the parasites on the host. The *Rhabdochona* sp. heavy intestinal infections. 1 host (21 worms) is likely to result in local inflammation, mucosal erosion, and deficiency of nutrient absorption, which has downstream effects on growth and condition factor. With its thorny proboscises acanthocephalans can produce local necrosis of the gastric wall or the intestinal wall. Gall-bladder trematodes like *Thaparotrema pedicellatum* can disrupt bile movement and lipid digestion, and *Isoparorchis* in the swim-bladder can disrupt buoyancy control in fish infested with many worms. Carp aquaculture has known even sub-clinical infections over time, which reduce fecundity and depress growth - direct effects which are directly translated into fishery yield.

There are biochemical effects of helminth infection of major Indian carps reported in associated host-parasite systems. Kumar [22] demonstrated that infection of *Catla catla* and *Labeo rohita* by the acanthocephalan *Pallisentis nagpurensis* considerably changed protein and free amino acid metabolism, as there was muscle protein content reduction and altered amino acid profile in the liver. Analogically, the *Dispirin* and intestinal infections cured here will, respectively, have similar, but taxon-specific metabolic costs. Histopathological studies in West Bengal [27] have described tissue-level evidence of epithelial injury, oedema, and inflammatory cell involvement in the intestines and gills of parasitically infested major carps, which can be used to compare future Indus-system data against. The current sample is too small to allow a quantitative analysis of host condition, but the qualitative prediction is that

infected *Catla catla* in the Kotri reach will show some combination of decreased growth efficiency, altered metabolism, and (in the most heavily infected animals) the presence of organ-level pathology.

6.2 Public-Health Concerns

The most impactful result of this paper, as far as food-safety is concerned is the occurrence of *Echinochasmus* in the intestine of *Catla catla*. Several species of *Echinochasmus* are known food-borne zoonoses; humans become infected by eating raw or undercooked fish meat containing infective metacercariae resulting in echinociasmiasis - an intestinal trematode infection with abdominal pain, diarrhoea and impaired nutrient absorption [46]. The current specimens are adult worms found in a definite fish host (not in the infective stage which infects humans), but their occurrence in the local ecosystem means that infective-stage worms are present. This, in a region where *Catla catla* is a popular food, and where the methods of preparation do not necessarily include thorough cooking (particularly of traditional foods), is a quantifiable, although imprecisely measured, community-health hazard.

Risk reduction recommendations come as a logical conclusion. (i) The authorities in charge of public health ought to provide explicit instructions on the temperatures and the duration required to cook meat that will render metacercariae inactive. (ii) Parasitological screening of fish-market should be incorporated in the inspection of fish-market especially at the times of high transmission. (iii) Consumer education campaigns- via media available to fisher communities and small-scale traders- would enable bridging the knowledge gap between household practice and the science.

6.3 Implications for the Indus Fishery

In fisheries-management terms the overall theme of the analysis presented here is that, with a modest sample of fish ($n = 26$), a well-organized, multi-taxon parasite community spanning all three major helminth groups is evident. This implies that systematic surveillance (a combination of morphological identification and molecular diagnostics) would have fast payoffs on the inland fishery sector in Sindh. Certain measures to be considered are:

- It should be instituted a regular parasitological surveillance programme at key landing areas along the Kotri reach, and seasonal sampling to represent the change across time.
- Education of fisheries extension personnel on the fundamental methods of identifying parasites and microhabitat analysis, such that the suspected fish can be identified at initial observation.
- Liaising with avian ecologists to keep track of the parasite burden of piscivorous birds on the river a low-utilized but high-yield indicator of transmission pressure.
- Connecting parasitology to aquaculture extension to guarantee that wild stock infected is not used as broodstock in the hatchery where the parasites may become amplified and reduce the quality of seeds.

6.4 Linking Parasitology to Food Security

Inland fisheries in Pakistan are a source of dietary protein in rural and peri-urban areas and *Catla catla* is among the most readily available and inexpensive sources of protein to low-income families in Sindh. The parasite-induced losses are not abstract, in relation to food-security. A 10% decline in marketable yield caused by parasitic infection - a conservative estimate based on prevalence and intensity values herein reported - would result in a loss of thousands of tonnes of fish to the Indus capture fishery annually, with unequal effects on consumers with the least capacity to replace alternative protein sources. On the other hand, each unit of investment in parasite surveillance, public-health education, and aquaculture biosecurity have quantifiable returns in terms of yield saved and less clinical burden. On these grounds the argument that parasitology should be an issue of fisheries-policy, and not an object of scholarly interest, is clear-cut.

7. Comparison with Other Studies

The ecological reading of the data is enhanced by placing the Indus which leads to a wider comparative context. Both *Catla catla* have been surveyed in West Bengal [19] and Andhra Pradesh [6, 28] have reported an overall helminth prevalence of the 25-45% range - which covers the 34.6% in this case. Generally, trematodes have dominated these studies and partitioning of

microhabitats on a broad scale is like what is observed in the present study with intestinal forms represented in the majority. The occurrence of isoparorchis in carps in Indian waters has been more common than the earlier association of the genus with siluriform fishes [43-45] would suggest and the interpretation is that *Catla catla* can be an alternative or paratenic host of the genus.

A complementary frame is given by the Pakistani research done on the freshwater fish helminths in other rivers and lakes. Mixed parasitic infections of fishes in the Indus River at D.I. Khan have been reported by Tayyab et al. [15] that includes nematodes and trematodes taxa that overlap in genus with those in the present material. The Ayaz et al. [16] reported the endoparasites of River Punjkorha in Khyber Pakhtunkhwa where the nematodes in the intestines seemed to predominate in the most affected hosts. The acanthocephalan fauna of Sindh, of which *Neoechinorhynchus* spp. were known only by Bilqees and others in Haleji Lake, are now supplemented by the current record of *Dispirin* sp. in *Catla catla* of the Indus River - the first record of this genus in Pakistan.

Three strong comparative observations are brought out. (i) The *Catla catla* helminth community structure of the Indus is concordant with other areas of South Asia, and confirms the inference that the surface- and mid-water feeding ecology of the host always causes it to be funneled into the life cycle of the trematodes. (ii) Intense nematode infection of individual hosts - as is the case with *Rhabdochona* sp. - has been reported previously both in Indian and Pakistani literature, and indicates that the presence of aggregated nematode parasite loads is a common occurrence not a sampling artefact. (iii) The diversity of the Acanthocephalan parasites of *Catla catla* seems to be regionally diverse with new genera still being introduced with each geographic area surveyed - a very strong case to expand sampling in the Indus system.

7.1 Parasites as Bioindicators of Ecosystem Health

In addition to their direct disease-causing effects, helminth parasites are becoming important bioindicators of the health of aquatic ecosystems.

Even the presence of a structured, multi-taxon helminth community in *catla catla* in the Kotri reach means that the ecological relationships that are necessary to maintain these life cycles (vast numbers of snail and copepod intermediate hosts, the persistence of piscivorous birds, and the maintenance of hydrological conditions) are intact. Trematodes especially, because of their reliance on several intermediate hosts, are good integrative indicators of community-level health: their occurrence is an indicator that the ecological web of the Indus at Jamshoro is functioning. On the other hand, present declines in the diversity of parasites may be an early indicator of habitat degradation, pollution, or hydrologic disturbance - something to remember with the growing stresses on the lower Indus of upstream water abstraction and pollution. Poulin [32, 33] has discussed in detail that a body of diversity of parasites indicates the structural integrity of the host community, and the current data is correlated to the larger body of knowledge.

8. Limitations of the Present Analysis

Several constraints deserve to be mentioned. First, the number of 26 hosts used, though sufficient to record the qualitative composition of the helminth community, is small to make quantitative inferences on prevalence and strength. The numbers reported here are therefore broadly bracketed by confidence limits and the low-frequency interactions or rare taxa may have been easily overlooked. Second, sampling was not seasonally stratified; the reported values are a pooled estimate of two years, and the seasonal variation, which is known to be high in fish helminth communities of subtropical river systems was not eliminated. Third, the current data are descriptive in nature of adult worms found in fish hosts and do not directly test the hypothesized transmission pathways: to confirm the involvement of intermediate-hosts, definitive-host-identity, and zoonotic transmissibility, complementary studies (snail surveys, bird parasitology, molecular linkage) are required. Fourth, no histopathology has been performed and thus the deduced host effects (mucosal erosion, dysfunction in the gall-bladder, swim-bladder compromise) are just possible expectations and not proven results.

The qualitative inferences above are not undermined by these constraints, and indicate that *Catla catla* in the Indus at Jamshoro is a structured multi-taxon helminth community with well-defined microhabitat separation and food-safety applicability, but provide the framework of the next stage of research.

9. Future Directions

The present analysis suggests four priority areas for future research:

- Sampling seasonally and over many years (at least 100 hosts) to narrow down the prevalence and intensity estimates and to describe the dynamic relationship between infection and monsoon flow, water temperature, and host condition.
- Molecular characterization of each of the six taxa with mitochondrial *cox1* and nuclear ITS or 28S rDNA loci, to verify species-level identifications, and to test for cryptic diversification in *Echinochasmus*, *Rhabdochona*, *Procamallanus* (*Spirocamallanus*), and *Dispirin*.
- Histopathological analysis of infected organs to determine the extent of damage caused by each parasite at the cellular and tissue level, which will give a direct correlation between parasitology and fish welfare or quality.
- Ecosystem studies where fish, snails, cope pods, and piscivorous birds are all sampled at the same location and enable transmission cycles to be empirically recreated, instead of being estimated based on analogy.

In addition to these technical priorities, there must be a larger translational agenda: the parasitological information produced must be used in fisheries advisory services, and in public-health communication, and in aquaculture extension, such that the scientific knowledge produced in the academia is translated into practice in the field. Such an integrated approach would stand to benefit the Indus fishery, and the millions of people who rely upon it.

10. Conclusion

The *Catla catla* host-parasite system of the Indus river at Jamshoro is organized around two main axes. First, the community of parasites is taxonomically diverse and ecologically structured: trematodes are common yet at low intensity, and

nematodes are common but at high intensity with acanthocephalans sporadic. Second, the distribution of parasites among microhabitats within the host is strictly segregated: there are gall bladder, body cavity/swim-bladder, intestine and stomach each hosting a particular taxon, with the intestine bearing the greatest collective load. These trends are in line with the ecology of surface and midwater feeding of the host, the local presence of intermediate hosts and the presence of piscivorous birds as definitive hosts in trematode life cycles. The reappearance of *Echinochasmus* - a genus that has been shown to have zoonotic potential - provides a valid food-safety issue and supports the argument of systematic parasite monitoring in the Indus fishery. The results presented herein offer an ecological basis on which future studies based on molecular, histopathological and management-related research can be tuned, and they underscore the importance of considering parasites of *Catla catla* as being part of a larger, Indus environment.

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