
Ecology of a diplozoon parasite on the gills of the African cyprinid *Barbus neumayeri*

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Abstract

In oxygen-deficient waters, the difficulties of oxygen uptake in gill parasites and their fish hosts may influence host and parasite densities, site selection by the parasite, and effects of the parasite on host condition. This study quantified the prevalence and intensity of the gill monogenean *Neodiplozoon polycotyleus* in the African cyprinid fish *Barbus neumayeri* from an intermittent forest stream in western Uganda. Oxygen levels were low in the stream over the 12-month study, averaging only 2.5 mg litre⁻¹ (monthly range = 1.2–4.3 mg litre⁻¹). However, parasite prevalence was high (47.2%), suggesting high tolerance to low oxygen in *N. polycotyleus*. The prevalence of parasites varied with host body size, with the highest frequency of occurrence in the middle size classes. Prevalence also varied over the year; seasonal peaks of rainfall coincided with a lower frequency of *N. polycotyleus*. The significantly nonrandom frequency distribution of parasites among hosts suggests regulation of parasite numbers. Of the hosts infected, 37.1% harboured one *N. polycotyleus* parasite, and 62.9% harboured two parasites. No fish were infected with more than two diplozoons. There was evidence for strong site specificity by *N. polycotyleus* within hosts; 77.7% of the parasites were located on the filaments of the second gill arch, which may relate to increased oxygen availability. In addition, only one of the 178 infected fish had more than one parasite on one side of the branchial basket. Although *N. polycotyleus* is undoubtedly parasitic, we found no evidence of a negative parasitic effect on the condition or reproductive status of *B. neumayeri*.

Key words: Africa, Cyprinidae, hypoxia, *Neodiplozoon polycotyleus*, parasite

Résumé

Dans les eaux déficientes en oxygène, la difficulté que rencontrent les parasites des branchies et leurs poissons hôtes peut influencer la densité des hôtes et des parasites, la sélection du site par le parasite et l'effet du parasite sur la condition de son hôte. Cette étude quantifie la prévalence et l'intensité de *Neodiplozoon polycotyleus* chez le cyprinidé africain *Barbus neumayeri* dans un cours d'eau forestier intermittent à l'ouest de l'Ouganda. Le taux d'oxygène du cours d'eau est resté bas pendant les douze mois qu'a duré l'étude, égal en moyenne à 2,5 mg/litre (écart mensuel = 1,2–4,3 mg/litre). Cependant, la présence parasitaire était élevée (47,2%), ce qui suggère chez *N. polycotyleus* une très bonne tolérance à de faibles taux d'oxygène. La présence de parasites variait avec la taille, elle était la plus élevée dans les classes de taille moyenne. Cette présence variait aussi au cours de l'année, et les pics saisonniers des pluies correspondaient à une abondance moindre de *N. polycotyleus*. La distribution de fréquence des parasites qui n'est significativement pas laissée au hasard chez les hôtes suggère une régulation du nombre de parasites. Chez les hôtes infestés, 37,1% abritaient un parasite et 62,9% en abritaient deux. Aucun hôte n'en avait plus de deux. On a constaté l'évidence d'une forte spécificité de site de *N. polycotyleus* chez les hôtes: 77,7% des parasites se trouvaient sur les filaments de la deuxième branchie, ce qui peut avoir un rapport avec une meilleure disponibilité en oxygène. De plus, seul un des 178 poissons infestés avait plus d'un parasite d'un même côté. Bien que *N. polycotyleus* soit indubitable-

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ment un parasite, nous n'avons trouvé aucune preuve d'un effet négatif sur la condition ou sur le statut reproducteur de *B. neumayeri*.

Introduction

Most monogeneans parasitize gills of fish. Many of these occur on gill filaments, although some are located on gill rakers or the lateral surfaces of gill arches (Bychowsky, 1961). The group has been somewhat neglected ecologically, particularly in the tropics where studies have emphasized surveys of fish for infection and taxonomic considerations (Schmidt & Roberts, 1977; Ukoli, 1984). Nevertheless, monogeneans should be of great interest to ecologists because their simple life cycle produces a tightly linked ecological relationship between the eggs, larval stages, and definitive host.

The general impression in the literature is that little effect is produced upon the host when monogeneans occur in small numbers. However, when they attain high infection levels, a condition characteristic of overcrowded host populations (e.g. fishponds), they are usually pathogenic. Damage includes haemorrhages and ulceration of host epithelium, development of epithelial outgrowths, and production of excessive amounts of mucus, which can disturb the respiratory function of the gills and ionic exchange (Erasmus & Chapman, 1972; Ukoli, 1984). Heavy infection can also lead to anaemia in the case of those that feed primarily on host blood (Erasmus & Chapman, 1972).

The majority of monogeneans, being parasitic on gills, have access to abundant oxygen. However, some species live in oxygen-deficient habitats, and at least one monogenean exhibits a well-developed mechanism for obtaining oxygen (Smyth, 1966; Kearn, 1971). The effects of gill parasites on host condition and survival may be particularly important in these oxygen-scarce habitats where any loss in oxygen-uptake efficiency could be critical for the host.

Hypoxia is widespread in tropical fresh waters, particularly in heavily vegetated swamps, floodplain pools, flooded forests, and dry season pools of intermittent streams (Carter & Beadle, 1930a; Carter, 1955; Kramer *et al.*, 1978; Junk, Soares & Carvalho, 1983; Chapman &

Kramer, 1991). Although many fish that live in such habitats are air breathers (Carter, 1935; Carter & Beadle, 1930b; Carter, 1955; Chapman, 1995), many non-air breathers also survive by virtue of several different respiratory adaptations, including development of large gills that maximize oxygen uptake (Chapman & Liem, 1995). In oxygen-deficient waters, strong selection for low oxygen tolerance in gill monogeneans and their fish hosts may influence host and parasite density, parasite site selection, and effects on host condition.

In this study, we documented the prevalence and intensity of a gill monogenean in a small non-air-breathing cyprinid from an intermittent forest stream in western Uganda where oxygen availability is seasonally low. We focused on the way in which parasitism is partitioned across and within hosts and looked for effects of infection on host characters. Potential life history correlates of parasite prevalence were examined, including host size and sex, and parasite site specificity was described and considered in light of oxygen acquisition. We also looked for seasonal patterns in frequency of infection, which may relate to the strong seasonal pattern of habitat expansion associated with seasonal rains. To examine potential effects of the parasite on the host, we related host condition and reproductive status to the prevalence and intensity of infection.

Materials and methods

Study site and species

The ecological interactions between a gill parasite, *Neodiplozoon polycotyleus* Paperna, 1973, and its host, *Barbus neumayeri* Fischer 1884, were studied over a 13-month period in Kibale National Park, Uganda (0°13'–0°41'N and 30°19'–30°32'E). Approximately 60% of the park is moist evergreen forest; the remainder is a mosaic, swamp, grassland, plantations of pine, thicket, and colonizing forest. Kibale is drained by two major ever-flowing rivers, the Dura and the Mpanga rivers; both flow into Lake George and are fed by numerous small forest streams. The rivers consist of large ever-flowing channels peppered by valleys choked with papyrus (*Cyperus papyrus*) for hundreds of metres to several kilometres (Chapman & Liem, 1995).

Mean annual rainfall in Kibale National Park (1987–95) averaged 1660 mm (range = 1205–1940 mm). Rainfall is well dispersed over the year, but there are

distinct wet and dry seasons that are bimodal in pattern. May to August and December to February tend to be drier than other months, with the May to August dry season of longer duration than the earlier dry season in the year.

The study site was the Inlet Stream East, a small intermittent tributary of the Rwembaita Swamp, one of the park's larger papyrus swamps. The stream flows through swamp forest before entering the Rwembaita Swamp. Fish were collected from a 220 m stretch of the stream just prior to its confluence with the papyrus swamp. This section of the stream averaged 18 cm in depth and 155 cm in width during the early dry season. Flow is intermittent and associated with seasonal patterns of rainfall.

One of the two fish species inhabiting the Inlet Stream East is the small cyprinid *B. neumayeri*. This species reaches a maximum length of 11 cm in swamps and rivers of Kibale National Park. It is widely distributed in East Africa (Greenwood, 1962) and is found in a variety of habitats within Kibale including seasonal streams, papyrus swamps and ever-flowing streams and rivers. *Barbus neumayeri* feeds principally on insect larvae and aquatic plants (Corbet, 1961). In Kibale, *B. neumayeri* reproduces throughout the year, but reproductive activity peaks with seasonal peaks of precipitation when dissolved oxygen levels are relatively high (Chapman & Frankl, in press). *Clarias liocephalus* Boulenger 1898, an air-breathing clariid catfish (Clariidae), is the only other fish species in the stream.

Barbus neumayeri is parasitized by a diplozoan, a gill monogenean of the family Diplozoidae. Boeger & Kritsky (1997) present a revised hypothesis for the phylogeny of the monogeneans, in which the diplozoans are placed in the subclass Oligonchoinea and order Mazocraeidea, with the family falling in the suborder Discocotylinea. The biology of diplozoans is unusual, because two hermaphroditic individuals are united in permanent cross-copula (Ukoli, 1984; Le Brun, Renaud & Lambert, 1990). The diplozoans are all blood-feeding gill parasites of freshwater fish. The diplozoan parasitizing gills of *B. neumayeri* were identified using morpho-anatomical criteria as *Neodiplozoan polycotyleus* following Paperna (1973, 1979). However, it should be noted that Le Brun *et al.* (1990) express doubts as to the taxonomic value of morpho-anatomical characters for diplozoan identification and stress the need for genetic analyses. We therefore consider this identification as

tentative pending further taxonomic studies within the family. *Neodiplozoan polycotyleus* is known to parasitize the gills of *Labeo victorianus* from the Nzoia river in Kenya, *Barbus paludinosus*, *Barbus cercops* and *Barbus macrolepis* from the Ruaha River in Tanzania, and *Barbus kerstenii* from the swamps of Lake Kyoga (Paperna, 1979). Very little is known about the host-parasite interactions in diplozoans, except in *Diplozoan gracile* for which several factors have been demonstrated to affect host infestation in European populations, including schooling behaviour of the fish, diel patterns of host activity, and refuge zones where host and parasite are concentrated (Le Brun *et al.*, 1990).

Fish-parasite collections and environmental monitoring

Barbus neumayeri were collected with minnow traps set overnight in the Inlet Stream East monthly from June 1991 to August 1992 ($n = 13$ months). Each trap was placed so that its top extended above the water surface to permit *B. neumayeri* access to the surface film because this species uses aquatic surface respiration to meet its oxygen demands at low oxygen levels. A total of 377 *B. neumayeri* were collected over the study period with an average of 29 fish per month. Fish were preserved in formalin and transferred to 70% ethanol. For each fish, we recorded total length and weight, degutted weight, sex, state of gonadal maturity (modified from De Silva, Schut & Kortmulder (1985) and Hari-kumar *et al.* (1994) on a scale of I = immature to VI = spent), and gonad weight. To quantify infestation of *B. neumayeri* gills by *Neodiplozoan polycotyleus*, we removed the operculum from each side of each fish, and recorded the number of parasites and the gill arch of attachment.

Dissolved oxygen concentration and water temperature were recorded monthly in the Inlet Stream East over the period of investigation. Each month, duplicate samples of oxygen were recorded at four stations in the stream (11:00 and 14:00 hours) using a YSI meter (Model 51B). Rainfall data were available from the Makerere University Biological Field Station, which is about 3 km from the Rwembaita Swamp system.

Statistical analysis

The chi-squared test of independence was used to examine whether parasite prevalence was independent

of set, size and side of the branchial basket. To determine whether parasites were randomly distributed on the host, we compared the observed distribution of parasites on *B. neumayeri* to a random one, the Poisson distribution. The difference between these two distributions was evaluated with a chi-squared test.

Analysis of covariance was used to measure parasitic effects on host condition, i.e. host weight as a function of total host length. To assure a linear relationship between total length and weight, we log-transformed these variables. In addition, because variables other than parasitism may affect host condition, these other variables were also included in the covariance models, yielding the following set of independent variables: log total host length, number of parasites on the host, host sex, season of collection, and state of gonadal maturity (stages 1 through 6 according to De Silva *et al.*, 1985).

Analysis of covariance was also used in two ways to measure parasitic effects on host reproduction. First, parasitic effects on the total host length–host gonadal weight relationship were determined in a model with log gonadal weight as the dependent variable and log total host length, number of parasites on the host, host sex, season of collection, and state of gonadal maturity as the independent variables. Second, parasitic effects on the state of gonadal maturity were determined in a model with state of gonadal maturity as the dependent variable and log total host length, number of parasites on the host, host sex, and season of collection as the independent variables.

Results

Variance in parasitism among and within hosts

A total of 377 *B. neumayeri* was examined for the presence of *N. polycotyleus*, and 178 (47.2%) were infected. Of the hosts infected, 37.1% harboured one *N. polycotyleus*, and 62.9% harboured two parasites producing a mean intensity of 1.63 parasites per host.

The observed distribution of parasites on the host was found to depart significantly from random distribution ($\chi^2 = 125.16$, $P < 0.001$). The observed distribution had many fewer loads of one parasite, many more loads of two parasites, and many fewer loads of three or more parasites than did the random one (Table 1). Truncation of parasite loads at two parasites is evidence of under-

Table 1 Observed distribution of *N. polycotyleus* on the gills of *B. neumayeri*. A random distribution (Poisson) with the same mean and sample size of hosts as the observed distribution is shown also

Number of parasites	Observed number of host individuals	Expected number of host individuals
0	199	175.51
1	66	134.65
2	112	51.65
3 or more	0	16.22

dispersion, quite unlike the overdispersed nature of many parasite distributions (Williams, 1964).

Parasites were not partitioned equally among hosts. Although males and females were similarly infected (57.8% males/49.4% females, $\chi^2 = 1.14$, $P > 0.25$), parasite load varied with body size. The frequency of occurrence of parasites was lowest in the smallest size classes, higher in intermediate size classes and lower in the largest individuals ($\chi^2 = 71.94$, $P < 0.005$, Fig. 1).

There was evidence for strong site specificity by *N. polycotyleus* within hosts. All parasites were found attached to gill filaments (Fig. 2), but 77.7% of the para-

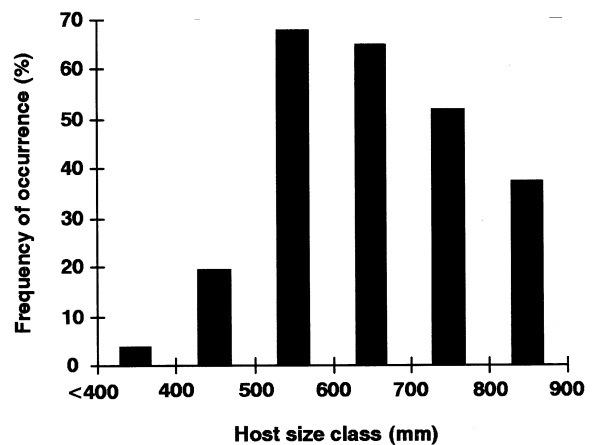


Fig 1 Prevalence (i.e. frequency of occurrence) of *N. polycotyleus* on gills of different size classes of its host *B. neumayeri* ($n = 377$ fish) from an intermittent stream in western Uganda (illustrated by Rebekah McClean)

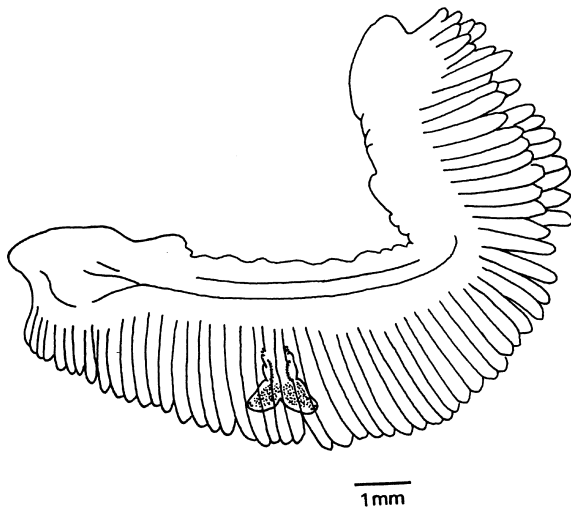


Fig 2 *Neodiplozoon polycotyleus* attached to the gill filaments of *B. neumayeri*

sites were located on filaments of the second gill arch (Fig. 3). The distribution of parasites did not differ between right and left sides of the branchial basket ($\chi^2 = 3.27, P > 0.1$): 80.1% of the infected *B. neumayeri* had a parasite on the second arch of the left side of the branchial basket, and 72.9% had a parasite on the second arch of the right side (Fig. 3). Only one of the 178 infected fish had more than one parasite on the same

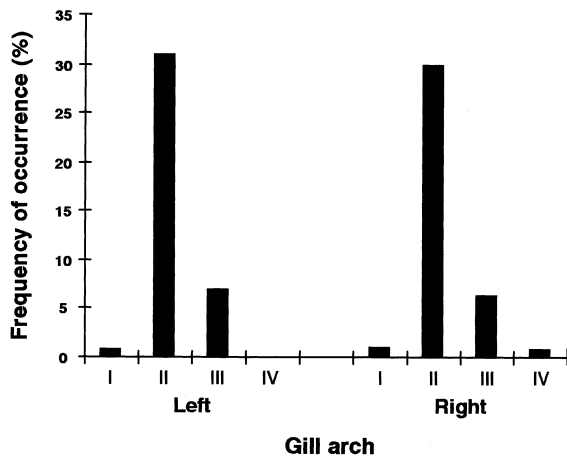


Fig 3 Differential use of gill arches of *B. neumayeri* by the monogenean, *N. polycotyleus*. Prevalence is expressed as the percentage of gill arches in a particular location (I, II, III, IV) infected with *N. polycotyleus*

side of the branchial basket; in all other cases of fish with two parasites, one parasite was on the left and the other on the right.

Seasonal changes in occurrence of Neodiplozoon sp.

Monthly oxygen levels were low in the Inlet Stream East over the period of study, averaging 2.5 mg litre⁻¹. The lowest values were recorded in February and April when oxygen fell to 1.2 mg litre⁻¹. Peak values were observed during seasonal flooding. The heaviest rains occurred in first rainy season of the sampling period (October and November 1991) when 582 mm of rain fell and oxygen levels increased to 4.3 mg litre⁻¹ (Fig. 4).

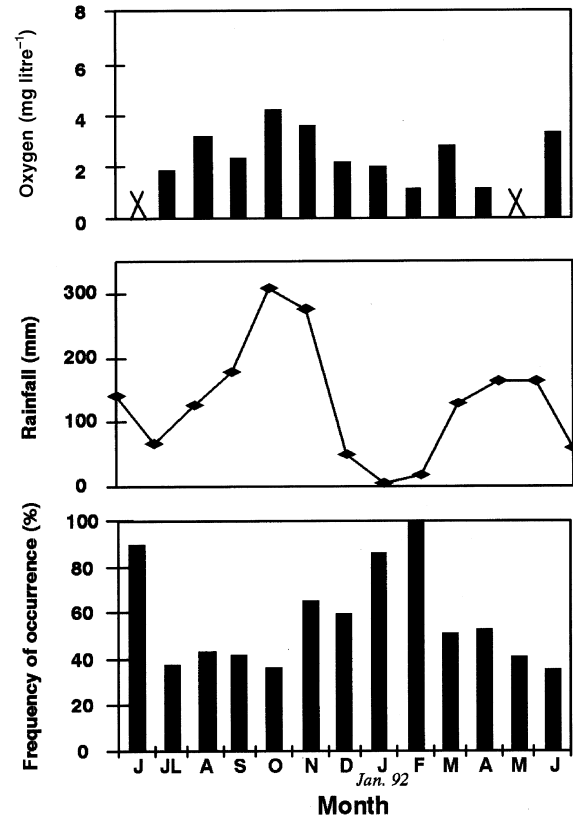


Fig 4 Seasonal changes (July 1991 to June 1992) in rainfall in Kibale National Park, dissolved oxygen in the Inlet Stream East where each value represents the average of duplicate samples from four stations in the upper 20 cm of water, and the prevalence of *N. polycotyleus* on the gills of *B. neumayeri*. Xs represent months when data were not available

Water temperature averaged 15.4°C (range = 13.1–18.4°C).

Seasonal changes in parasite prevalence were examined for fish greater than 500 mm (total length), because fish in smaller size classes had a very low prevalence of infection (Fig. 1). Infection of *B. neumayeri* with *N. polycotyleus* was found throughout the year in this group, but the prevalence of infection varied ranging from 36% in June (1992) to 100% in February (1992). Comparing patterns of parasite infection and rainfall suggests that seasonal peaks of rainfall coincide with lower prevalence of *N. polycotyleus* (Fig. 4).

Infection in relation to host condition and reproductive state

Parasites did not significantly affect the host length–weight relationship ($F = 0.67$, $P = 0.51$). The final covariance model, which accounted for 97.66% of the variation in the dependent variable log host weight, included these significant independent variables: log total host length ($F = 3491.15$, $P < 0.0001$), host sex ($F = 9.71$, $P < 0.0001$), state of gonadal maturity ($F = 6.71$, $P < 0.0001$), and the interaction between host sex and state of gonadal maturity ($F = 3.85$, $P < 0.001$).

Parasites also did not significantly affect the host length–gonadal weight relationship ($F = 0.27$, $P = 0.77$). The final covariance model, which explained 88.51% of the variation in the dependent variable log gonadal weight, included these significant independent variables: log total host length ($F = 12.27$, $P < 0.0005$), host sex ($F = 86.15$, $P < 0.0001$), state of gonadal maturity ($F = 6.54$, $P < 0.0001$), the interaction between host sex and state of gonadal maturity ($F = 25.75$, $P < 0.0001$), and the interaction between log total host length and state of gonadal maturity ($F = 4.92$, $P < 0.0001$).

Finally, parasites did not slow development of host gonads. In fact, the significant parasitic effect found was caused by parasitized fish having more mature gonads than did unparasitized fish of the same sex and total length. The final covariance model, which accounted for 53.50% of the variation in the dependent variable state of gonadal maturity, included these significant independent variables: log total host length ($F = 31.26$, $P < 0.001$), host sex ($F = 23.97$, $P < 0.001$), and number of parasites on the host ($F = 3.58$, $P = 0.029$). There were no significant seasonal effects in

these three analyses, which may reflect differences in the numbers of smaller individuals present in different months.

Discussion

Life history and environmental correlates of parasitism

Fish body size and age have often been found to be positively associated with the prevalence and/or intensity of parasite infection (Dogiel, 1961; Betterton, 1974; Madhavi & Rukmini, 1991; Chandler, Chapman & Chapman, 1995). Life span of the host, *B. neumayeri*, has not been determined in the field, but lab-held fish have survived more than 3 years. Although we do not know the life span of *N. polycotyleus*, the diplozoan *Diplozoan paradoxus* lives more than 2 years (Bychowsky, 1961). A long life span of parasite and host could cause more hosts to be parasitized with age or could cause a higher parasite load with age. However, parasite prevalence increased with host body size only up to 700 mm; larger individuals showed lower prevalence. Such a pattern could reflect the premature mortality of infected older individuals (Pennycuick, 1971; Anderson & Gordon, 1982; Gordon & Rau, 1982). However, given the underdispersion of parasites in the *B. neumayeri* population and no evidence for a significant negative effect of parasite infection on host condition, we feel it unlikely that larger parasitized individuals exhibit lower survival than do nonparasitized fish. Alternatively, the lower prevalence in larger individuals may be due to the development of immunity with age.

Seasonal peaks of rainfall coincided with lower prevalence of *N. polycotyleus*. A higher frequency of occurrence in the dry season may result from relatively higher host susceptibility. Organisms under stress or in poor body condition are generally less resistant to parasites (Zuk, 1990). In seasonally flooding waters, dry season conditions lead to habitat contraction, lower oxygen availability, higher fish densities, and in some cases lower fish condition and higher mortality (Chapman, Kramer & Chapman 1991; Lowe-McConnell, 1964; Chapman & Chapman, 1993a,b). In the Inlet Stream East, water availability is much reduced during the dry season, and sections of the stream are isolated by land barriers. This leads to concentrations of *B. neumayeri* in dry season refuges. If higher densities contribute to higher levels of stress, dry season conditions may lead to

higher levels of parasitism. Chandler *et al.* (1995) found host density to be a significant predictor of the prevalence of 'diplostomulum' in the poeciliid fish *Poecilia gillii*, in isolated pools of a dry forest stream. They suggest that the high densities of *P. gillii* in some pools may induce high levels of stress as the dry season progresses. Higher densities of the host may also lead to higher prevalence of infection by increasing host availability. Le Brun *et al.* (1990) found that *Diplozoon* larvae spend about 60% of their lifetime on river bottoms, favouring infestation of benthic hosts. *Barbus neumayeri* is active throughout the water column, but tends to spend much time hidden under rocks and other bottom materials. Activity decreases during the dry season (Chapman & Liem, 1995), which probably leads to increased time near the bottom. In addition, the much reduced water flow during the dry season may pose less difficulty for the small swimming parasitic larvae. Le Brun *et al.* (1990) noted lower prevalence of *Diplozoon gracile* in large deep rivers with rapid current than in smaller tributaries. They attributed this pattern to higher host-finding abilities for the larvae in slower flowing waters.

Parasite dispersion

In all seasons *N. polycotyleus* were underdispersed in their hosts, which effectively reduces the number of fish suffering the consequences of heavy infestation. In our study, no fish was recorded with more than two parasites. This differs from the results of Le Brun *et al.* (1990) on the infection of four cyprinids by *Diplozoon gracile*. For at least two of the cyprinid species, numbers of parasites exceeded two in some hosts. Whether our results for *N. polycotyleus* are simply the result of the infection process (i.e. relative availability of hosts to parasites) or reflect a density-dependent mechanism for regulation of parasite numbers is not clear. However, the pattern of dispersion did not differ between the dry season when parasite transmission may be facilitated by high host density, and the wet season, when parasite transmission may be hindered by low host density and high current. This suggests that some mechanism for regulation of parasite numbers may exist.

Hypoxia tolerance and site specificity

Monthly oxygen levels were low in the stream over the 13-month study, averaging 2.5 mg litre⁻¹ with levels of

1.2 mg litre⁻¹ in February and April. However, parasite prevalence was high, averaging 47.2% and reaching 100% in February when oxygen concentration was very low. This suggests high tolerance to low oxygen in *N. polycotyleus*. This prevalence of infection is well within the range recorded by Le Brun *et al.* (1990) for *Diplozoon gracile* parasitizing four cyprinid species from well-oxygenated sites (River Herault, France). Although most monogeneans have been recorded from well-oxygenated habitats, some species do live in oxygen-deficient waters. For example, Paperna (1964) reported high tolerance to hypoxia in *Dactylogyrus extensus* infesting carp (*Cyprinus carpio*) reared in artificial ponds in Israel, and noted that tolerance is much lower in populations occurring in northern regions where the parasite is indigenous. Mechanisms compensating for hypoxia have been studied in *Entobdella soleae*, a monogenean found on the ventral surface of the common sole (*Solea solea*). The bottom-dwelling habits of the sole position the parasite in a medium of low oxygen tension. *Entobdella soleae* undulates its body to increase water flow under the sole, with the undulation rate inversely proportional to the oxygen content (Smyth, 1966; Kearn, 1971). Other behavioural mechanisms noted in monogeneans include site selection to maximize oxygen uptake efficiency.

Microhabitat specificity is widespread among monogeneans and is effected in several ways. There may be restriction to certain gill arches, to certain parts along the gill filaments, to the external or internal filaments, or to the right or left gills (Bychowsky, 1961; Rohde, 1979). In our study, we focused on site selection among the arches and side of the fish. *Neodiplozoon polycotyleus* parasitizing gills of *B. neumayeri* exhibited strong site selection: 77.7% of the parasites were on filaments of the second gill arch, and there was no significant difference in microhabitat specificity between right and left gills. Evidence for habitat selection as the factor underlying habitat specificity in parasites has been reviewed by Ulmer (1971). In many cases there is evidence for active site selection by the parasite. Holmes (1972) reviewed the importance of site selection in parasitic helminths and hypothesized that antagonistic interactions between parasite species in the same host may be expressed as direct competition or as interactive segregation. It cannot be ruled out that the evolutionary history of the *N. polycotyleus*–*B. neumayeri* relationship involved other interspecific competitors, which led to

the narrow niche specificity currently observed. However, Rohde (1979) reviewed several studies of monogeneans in which microhabitats were extremely restricted, although competing species were not currently present and probably did not exist in the past. Rhode argued that intrinsic factors play some role in determining niches in these species and suggested that narrow microhabitats may function to enhance the chance of locating a mate. In diplozoons, larvae that fail to find a partner subsequently die (Smyth, 1966), which may impose strong selection pressure to maximize the probability of intraspecific contact. Site specificity in monogeneans may also result from physico-chemical requirements. For *N. polycotyleus* in the hypoxic waters of the Inlet Stream East, selection of the second gill arch may place the parasite in an area of maximum laminar flow in the gill. Site selection in relation to oxygen availability has been observed in the monogenean *D. solidus*, which alters its selection of gill arches and position on the arch in response to decreased oxygen concentration (Bychowsky, 1961).

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