Can host body size explain the parasite species richness in tropical freshwater fishes?

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Summary. The variability of monogenean gill ectoparasite species richness in 19 West African cyprinid species was analyzed using the following seven predictor variables: host size, number of drainage basins, number of sympatric cyprinid species, host diversity, association with mainland forest, host ecology, and monogenean biological labelling. The size of the host species accounted for 77% of the variation in the number of parasite species per host, and host ecology an additional 8%. Together the effects of host size and host ecology accounted for 85% of the variation in monogenean species richness. This study shows that the deciding factors for explaining monogenean species richness in West African cyprinid fishes are host species size and host ecology. These results were compared with main factors responsible for parasite species richness in fish communities. Other possible explanations of monogenean community structure in west African cyprinids are discussed.

Key words: Species richness – Parasite communities – Freshwater fish – Body size – West Africa

Very few studies have tried to analyze possible reasons for the organization of parasite communities and species distribution. Several parasitological investigations have attempted to explain the structure of parasite communities using arguments that are sometimes quite different. Kennedy (1976) suggested that chance is an essential contributor to parasite community structure. Brooks (1980, 1988) and Mitter and Brooks (1983) considered that an essential role is played by the history of host-parasite relationships, i.e. host speciation is reflected in parasite cospeciation. Rohde (1979, 1989) proposed that parasite species accumulate in host species without saturating ecological niches. Price (1987) hypothesized a turnover of parasite fauna that never reaches equilibrium. New parasite species are recruited, which drive out

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resident species. Price and Clancy (1983) and Price (1990) have related parasite species richness to the range of the host species, and suggested for parasites the existence of dynamic equilibrium in hosts. These different causes, which are sometimes antagonistic, appear to correspond to particular circumstances that depend on the relative ecological complexity of host-parasite systems.

Using the model of monogenean Dactylogyridea in West African cyprinid fishes, we attempted to find the cause or causes that best account for the structure of the parasite communities observed. The results are criticized with the two main investigations on parasite species assemblages in fish i.e. Price and Clancy's (1983) study on British freshwater fish and Rohde's (1989) study on marine scombrid fish. Then, we examine what other ecological and evolutionary factors may also affect the structure of parasite communities in tropical freshwater fishes.

Materials and Methods

Data

The 19 species of cyprinids studied here are those most frequently caught in West Africa (Lévêque et al. 1990). Eight variables were tested in each of the 19 species (Table 1).

1. *SR*: Species richness of monogenean gill parasites. The list of gill parasite species found in each host species is taken from previous work (Guégan et al. 1988, 1989; Guégan and Lambert 1990, 1991). Some monogenean species were too scarce in the host species to allow a description (*Labeo coubie*, 1 species; *Labeo rouaneti*, 1 species). However, we have taken these nondescribed species into account in the calculations of species richness.

2. *ML*: The maximal standard length of fish observed by hydrobiologists of ORSTOM (Lévêque et al. 1990; Lévêque and Guégan 1990, Paugy et al. 1990a).

3. *NB*: Number of drainage basins where the cyprinid species is present. Biogeographic data are taken from Lévêque et al. (1990).

4. *HD*: Host diversity. The number of host species in each cyprinid genus was calculated for the west part of Africa according to Lévêque et al. (1990). This variable appears to be interesting for testing the role of host diversity on parasite species richness as

Table 1. Untransformed data for the 19 cyprinid species studies. Variables are as follows: *SR*, parasite species richness; *ML*, maximal length of host species; *NB*, number of basins; *NCYPS*, number of sympatric cyprinids; *HD*, host diversity; *DF*, distribution of fishes with mainland forests; *EH*, ecology of host species; *BLM*, biological labelling by monogenean species. *Nb* is the number of individuals analysed in each host species

Host species	SR	ML (mm)	NB	NCYPS	HD	DF	EH	BLM	Nb
L. coubie	13	497	18	16	8	1	2	1	49
L. senegalensis	8	400	13	12	8	1	2	1	35
L. roseopunctatus	2	260	02	07	8	1	2	1	43
L. rouaneti	5	360	01	04	8	2	3	1	19
L. parvus	2	190	18	14	8	1	3	1	33
L. obscurus	3	350	11	06	8	2	3	1	24
L. alluaudi	2	150	03	05	8	2	4	1	21
B. bynni occidentalis	4	365	07	09	7	1	2	2	21
B. bynni waldroni	4	280	05	05	7	2	2	2	12
B. petitjeani	7	220	02	06	7	2	2	2	29
B. sacratus	7	256	12	07	7	2	2	2	21
B. wurtzi	6	212	15	11	7	1	2	2	14
B. parawaldroni	7	230	06	06	7	2	2	2	11
R. senegalensis	1	180	13	11	5	1	1	3	28
R. steindachneri	1	125	11	06	5	2	1	3	19
R. nigeriensis	1	103	07	08	5	1	1	3	8
L. niloticus	0	63	08	12	5	1	1	0	16
G. waterloti	0	60	02	10	5	1	4	0	21
C. bibie	0	43	04	11	1	1	1	0	16

demonstrated on ectoparasite copepods of the marine fish family Scombridae (Rohde 1989).

5. *NCYPS*: Number of cyprinid species that are sympatric with a given cyprinid. The results were obtained from recent data on fish communities in West Africa (Teugels et. al. 1988; Lévêque et. al. 1989, 1990; Paugy et. al. 1990b). This variable appears to be fundamental since the probability of lateral transfers of parasites, affecting the structure of communities, increases with the number of sympatric and phylogenetically related host species (Kuris et. al. 1980; Guégan and Agnèse 1991).

6. *DF*: Distribution of cyprinid species in relation to forests. The percentages of forests associated with each drainage basin are from Hugueny (1989a, b). The distribution of each cyprinid was indexed according to its association with mainland forest. Two classes were defined: 1, species not closely associated with forests, 2, species found in forests.

7. *EH*: Ecology of the host species. Four attributes were indexed, based on the ecology of each cyprinid (Lauzanne 1988): 1, species living at the top of the water column, feeding near the surface, 2, species living generally in the middle of the water column, 3, species living at the bottom of the water column, feeding on algal cover generally among rocks, and 4, species living in strong currents.

8. *BLM*: Biological labelling by monogeneans. Four attributes were indexed: 0, no parasites; 1, host species parasitized by *Dactylogyrus*; 2, species parasitized by *Neodactylogyrus*; and 3, species parasitized by *Ancyrocephalus*.

The 3 qualitative variables *DF*, *EH*, and *BLM* were used as dummy variables which each had a value of 0 or 1 (Draper and Smith 1966). This transformation permits us to test the effect of belonging to a category on the regressions. For this, *DF* was replaced by one dummy variable (*DF*1), *EH* by three dummy variables (*EH*1, *EH*2, *EH*3), and *BLM* by three dummy variables (*BLM*1, *BLM*2, *BLM*3). Variable *DF*1 is 0 if the host species is not associated with forests, 1 if it is. Variables *EH*1, *EH*2 and *EH*3 are 0, 0, 0 if the host species is living at the top of the water column, 1, 0, 0 if living in the middle of the water column, 0, 1, 0 if living at the bottom and 0, 0, 1 if living in strong currents. Finally, variables *BLM*1, *BLM*2 and *BLM*3 are 0, 0, 0 if the host is not parasitized, 1, 0, 0 if the host species is parasitized with *Dactylogyrus*, 0, 1, 0 if parasitized with *Neodactylogyrus* and 0, 0, 1 if parasitized with *Ancyrocephalus*. These previous dummy variables were included or withdrawn from the model together.

Statistical methods

Two statistical analyses were carried out: simple linear regression and multiple regression. The variables "species richness" (*SR*) and "maximal length" (*ML*) were selected on the basis of results obtained in the analysis of correlation coefficients (Table 2). The contribution of different independent variables (or predictor variables) to the dependent variable (species richness) was then analyzed using the multiple regression method. Out of the three existing multiple regression methods, we chose the stepwise method since it combines the advantages of the other two methods (progressive and retrograde) while eliminating their disadvantages (Scherrer 1984). When a new variable is introduced into the model, the contribution of the previously chosen variables is systematically reexamined. At each step, the variable showing the highest partial correlation coefficient is included in the model if its significance is greater that 0.05. Partial correlation coefficients of the previous variables introduced in the model are systematically examined as proposed by Dagnélie (1973). When no more variables can be added to the model, the procedure for selecting variables is stopped.

The quality of the model was evaluated by analyzing residual variation (observed values minus the values predicted by the regression model). Variation was measured by calculating the index $Dev. = $ sum of squares $[e(i)-e(i-1)]$ with $e(i) = S_i - \hat{S}_i$ where S_i is the number of species observed in the ith host species and $\hat{S}_i$ is the corresponding predicted species number based on either equation. The principle is to test, against the null hypothesis H_0 of residual distribution according to a normal central limit law, whether the residuals tend to be more dispersed than predicted by chance, which would indicate a lack of linearity. Since no test is entirely satisfactory (Draper and Smith 1966), the quality of the model was evaluated by visual examination of residuals (Hugueny 1990).

The *VIF* variance inflation factor which gives an estimate of the increase of regression coefficient variance of one of the predictor variables due to near colinearity with the other variables was calculated according to Hugueny (1989).

Statistical analyses were carried out using the program BIOMECO Vr3,90, produced by the CEFE–CNRS ("Analyse Statistique et Modélisation des Processus Ecologiques", route de Mende, BP 5051, Montpellier, France) and marketed by AVENIX–FRANCE.
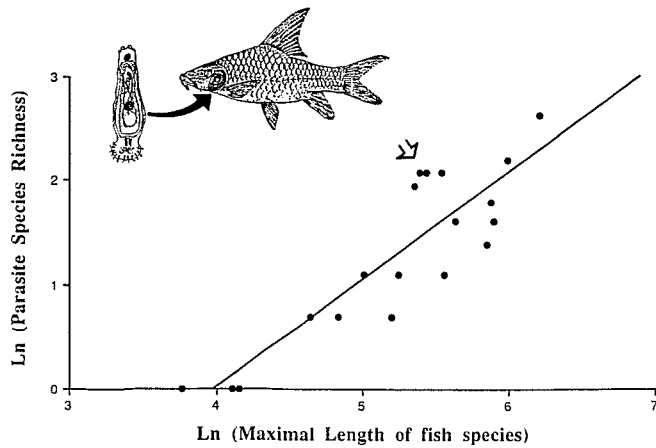
Fig. 1. Relationship between parasite species richness and maximal length (mm) of host species in 19 West African cyprinid species. The follow *arrow* indicates cyprinid fish genus *Barbus* from the Guinean refuge area (see text)

Table 2. Relationships between parasite species richness and maximal lengths of hosts

Variables	Intercept	Slope	r	r^2	F	Dev.
SR–ML	−1.085	0.021	0.786	0.617	27.43[1]	92
*SR–*ln*ML*	−15.508	3.678	0.740	0.547	20.54[1]	96
ln*SR–ML*	0.095	0.005	0.831	0.691	37.96[1]	4
ln*SR–*ln*ML*	−4.055	1.020	0.880	0.770	58.26[1]	2

SR, monogenean species richness; *ML*, maximal length of host species; r, correlation coefficient; r^2, determination coefficient; *F*, *F*-test; *Dev.*, test of residuals (best models are indicated by *Dev.* statistics in italics)

[1] $P < 0.0001$

Results

Relationships between parasite species richness (SR) and maximal length of hosts (ML)

After controlling for the effect of study effort, best fit was obtained by the power relation after double transformation of the data by Neperian logarithms (Fig. 1). This also gave a significant *F*-test result (Table 2). The best distribution of residuals was obtained in the relationships ln*SR–ML* and ln*SR–*ln*ML* where *Dev.* showed very little deviation from zero (Table 2).

Multiple regression

The body length and species richness variables were integrated into the analysis after transformation to Neperian logarithms to ensure a linear relationship between then.

Logarithmic transformations of all other variables did not significantly change the results. These variables were retained untransformed in the analysis.

Table 3 shows the correlation matrix between different variables used in the analysis. Some predictor variables were highly intercorrelated. The strong colinearity between certain predictor variables suggests that classic multiple regression should be examined and interpreted somewhat cautiously.

The multiple correlation coefficient is highly significant (Table 4). The method selected ln*ML* and *EH* and stopped at this step. None of the other variables showed a significant contribution. The function integrating ln*ML* and *EH* is assumed to be a predictor of ln*SR*. The log of the body length and the host ecology both contribute signicantly to the variation of the log of parasite species richness (Table 4).

Examination of residual variation in the model provided no basis for rejecting the null hypothesis of random distribution of residuals as a function of predicted values (see Table 4). Graphic examination showed a certain linearity of values indicating that the distribution of residuals was satisfactory (Fig. 2). The maximum variance inflation factor was not more than 4, indicating low colinearity between the predictive variables (Table 4).

Table 3. Correlation matrix of the variables used in multiple regression analysis

	ln*SR*	ln*ML*	*NB*	*NCYPS*	*HD*	*DF*1	*EH*1	*EH*2	*EH*3	*BLM*1	*BLM*2
ln*ML*	0.86[6]										
NB	0.30	0.31									
NCYPS	−0.06	−0.10	0.67[4]								
HD	0.70[5]	0.82[6]	0.19	−0.16							
*DF*1	0.32	0.26	−0.31	−0.81[6]	0.29						
*EH*1	0.75[6]	0.60[3]	0.10	0.01	0.43	0.04					
*EH*2	0.07	0.27	0.14	−0.10	0.36	0.21	−0.41				
*EH*3	−0.33	−0.36	−0.37	−0.13	−0.01	0.05	−0.32	−0.15			
*BLM*1	0.30	0.50[1]	0.16	0.09	0.64[4]	0.01	−0.07	0.57[2]	0.09		
*BLM*2	0.52[1]	0.30	−0.06	−0.29	0.18	0.34	0.72[5]	−0.29	−0.23	−0.52[1]	
*BLM*3	−0.34	−0.23	0.16	−0.05	−0.38	−0.08	−0.41	−0.19	−0.15	−0.33	−0.29

SR, species richness; *ML*, maximal length of host species; *NB*, number of basins; *NCYPS*, number of sympatric cyprinid species; *HD*, host diversity; *DF*, distribution in relation to forests; *EH*, host ecology; *BLM*, biological labeling by monogeneans (see text)

[1]: $P < 0.05$; [2]: $P < 0.025$; [3]: $P < 0.01$; [4]: $P < 0.005$; [5]: $P < 0.001$; [6]: $P < 0.0005$

Table 4. Multiple regression of ln (monogenean gill parasite species richness) versus the two significant predictor variables ln (maximal length of host species) and (ecology of host species). Coefficients are estimated by the least-squares method

Coefficients

lnML	EH1	EH2	EH3	Intercept	R	R²	F-test	Dev.	VIF
0.917[1]	0.499[2]	0.021	0.170	-3.790	0.925	0.855	20.68[1]	0.543[2]	3.85

ML, maximal length of host species; EH1, EH2 and EH3, dummy variables related to host species ecology; R, multiple correlation coefficient; R², multiple determination coefficient; F, F-test; Dev., test of residuals; VIF, variance inflation factor
[1] $P < 0.001$; [2] $P < 0.01$
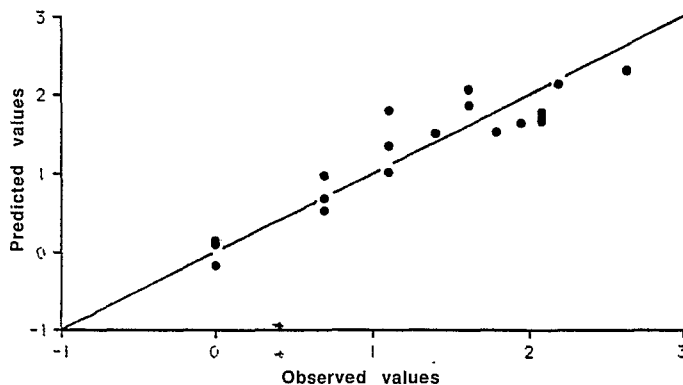
Fig. 2. Relationship between the number of monogenean species observed in 19 cyprinid species and the number of monogenean species predicted by the following model: ln(monogenean species richness) = 0.918 ln(maximal length of host species)+0.499 EH1+0.021 EH2+0.170 EH3–3.790. The *straight line* represents points at which the predicted value equals the observed value (Chi square=0.121; $P < 0.001$)

Discussion

The main results of the present study can be interpreted on the basis of several ecological and/or evolutionary hypotheses generally used to explain parasite community structure.

Hypothesis of a positive relationship between parasite species richness and host range

In a study of helminth fauna in freshwater fishes of the British isles, Price and Clancy (1983) demonstrated a positive relationship between the number of parasite species and the host species range (in km²): 68% of the variability of parasite species was explained by the host range. Fish species with a small range, on the study scale, also had the fewest parasite species. Inversely, host species with a large range had the largest number of parasite species. Price (1990) interpreted the results in the framework of the island theory of MacArthur and Wilson (1963, 1967) expressed as follows: as the host range increases, the probability of colonization by new parasite

species also increases; the extinction rates are higher in host species with small ranges; the immigration rates are also lower.

The 19 West African cyprinid species we have analyzed showed a positive relationship between monogenean species richness and host species body size. These results differ from those of Price and Clancy (1983), in which host range best accounted for parasite species variation. Host size was not a very satisfactory factor in their study. How can this contrasting information be reconciled?

The size of a species is often highly correlated with its range, i.e. the largest animals historically show the widest distribution (Mayr 1974; Gould 1984; Futuyama 1986) except for cases of island gigantism (Thaler 1973). Concerning West African freshwater fishes, Hugueny (1990) shows a positive species size – number of colonized drainage basins relationship. In the present parasitological study, the body sizes of cyprinid species are not clearly related to their ranges in Africa. The species *Labeo coubie*, which is the largest West African species, is indeed the most widely distributed (Lévêque et. al. 1990). On the other hand, some species such as *Barbus petitjeani*, which are of medium size in our study, have a rather small range, i.e. the upper courses of the Niger and Senegal rivers (Lévêque and Guégan 1990; Lévêque et. al. 1990). According to the hypothesis of a Guinea refuge zone proposed by Hugueny (1989a, b), fish populations that were once widely distributed took refuge in regions more favorable to their survival during the last ice ages. Finally, small cyprinids such as *Raiamas senegalensis* are also widely distributed in West Africa.

In the present study, the variable that best accounts for monogenean species variability is host body size (Table 2), but it is very difficult to relate it directly to the range of West African cyprinid species. Moreover, assessing relationships between parasites and range for fish must remain a matter of speculation: a work in progress (Guégan and Kennedy) demonstrates that the positive parasite species richness-host range relationship for fishes as proposed by Price and Clancy (1983) is undoubtedly spurious. Historical and ecological factors are probably responsible for the current distribution of monogeneans in the West African cyprinid fishes.

Hypothesis of host ecology

The results of multiple regression show that the variation in parasite species richness between individuals of different host species is not only caused by host size differences. The ecology of each host species affects parasite species richness significantly and the effect is cumulative with the first variable.

In general, species of the genus *Barbus* and several species of the genus *Labeo*, all of which live in the middle of the water column, show high parasite species richness. Cyprinids living at the top of the water column near the surface show little (such as *Raiamas*) or no infestation (such as *Chelaethiops* and *Leptocypris*). Species of currents, such as *Labeo alluaudi* and *Garra ornata* show also

little or no infestation by monogenean species. There is no linear relation between the position of fish in the water column and number of parasite species: fish species living in the middle of the water column show a greater number of parasite species than any other fish species living at the top or near the bottom of the water column. All these following predictions are confirmed by the multiple regression analysis. The two factors regulating parasitism appear to be water currents and the distance between the source of the parasite larval stage and the potential host. Cyprinids living in currents can be parasitized, but the current acts as an ecoethological filter, preventing swimming larvae from reaching the hosts. Similarly, fish located near the surface are too far away for effective recruitment of larvae hatching from eggs on the bottom. These remarks are completely consistent with the concept of parasite specificity put forward by Euzet and Combes (1980): for a host-parasite relationship to occur, the parasite has to come into contact with the host (probability of contact), and then the parasite has to recognize it as a favorable environment and colonize it (compatibility of host and parasite genomes).

The results presented here confirm the role of host species ecology in determining gill parasite communities in West African cyprinids.

The model described above, relating $\ln SR$ to $\ln ML$ and EH, reveals the existence of residuals (see Fig. 2), which remain to be explained. Several hypotheses can be proposed.

Hypothesis of host diversity

In many host groups parasite diversity is greatest in taxa which have the greatest diversity ("Eichler's rule"). Rohde (1989) has shown that the rule applies to ectoparasite copepods of the fish family Scombridae. In this case, host diversity accounted for 93% of the variability in copepods. Rohde (1989) also found a significant relationship between number of copepod species and number of geographical areas as demonstrated by Price and Clancy (1983). However, the former relationship was far more important for explaining copepod richness. Body size had a really low effect on the copepod richness.

In our study, the number of host species in the different cyprinid genera is not the main factor to explain the monogenean species richness. Body size is far more important. How is it possible to explain these two contradictory results both derived from studies of ectoparasites? Generally, large fishes have a higher capacity of dispersion than small fishes (Policansky 1983; Hugueny 1990). In addition, some freshwater fishes which possess an accessory respiratory device like species of the genus *Clarias,* or capable of occupying a large range of habitats like some cyprinid species have better dispersion ability that explains their large geographic range (Bertin and Arambourg 1958; Lowe-McConnell 1969, 1988). It is also possible that species which used to be widespread now have only relict distributions. Such freshwater fishes distributed in different catchments in-

crease their probability of disrupting genetical exchanges between different populations forming new species even if we can generally assume that speciation events are faster in small species inhabiting smaller habitats that in wide ranging large species. This would confirm the relative high correlation we observe between $\ln ML$ and HD ($r = 0.82$, $P < 0.0005$). The positive host maximal length-host diversity relation would indicate at least in this case that large cyprinid fish genera (*Labeo, Barbus*) have higher numbers of species than small cyprinid genera (*Garra, Leptocypris, Raiamas*). Then, it would be possible that the two variables $\ln ML$ and HD work in synergy, larger fish catching more parasites since they have larger gill surface area and a larger number of parasites to settle on the gills. Nevertheless, host body length of cyprinid fish better explains the number of monogenean species than host diversity. This possibility does not seem to apply in Rohde's study where body size appears to be not significant. This is probably due to the particularity in marine systems (i) larvae of small fish species may be dispersed far from a dispersion centre (Barlow 1981), and (ii) the contacts between related fishes occur increasing the probability of (ecto)parasite transfers as suggested by Kuris et al. (1980). This may enhance the effect of host diversity (related to the probability of host switching) on parasite richness in marine fishes and mask relations between species richness and host size.

Future studies should collect more data and compare the evolution of parasite communities in fish in freshwater catchments analogous to islands and open marine systems.

Hypothesis of gill area diversity

Hugueny (1989a) considers that in its extreme formulation, range must play a role in habitat diversity, i.e. the larger the range, the higher the probability that a certain type of habitat will be represented there; consequently, the higher the probability that the associated fauna will be present. In other words, if range is accounted for in the analysis, habitat diversity should have no effect, since its information is already included in the range variable. Thus, Hugueny (1989a) considers that it is difficult to determine how habitat diversity is perceived by the taxa studied (discussed by Rohde 1989 for gill parasites), and to define a pertinent index.

In the case of diplectanid monogeneans infesting bass, however, Silan et al. (1987) showed the importance of gill biotope heterogeneity by investigating the effects of biotic (number of gill filaments, colonizable gill area) and physical factors (role of currents) on the functional structure of populations and communities (density- and intensity-dependent mechanisms). In this last case, it could be also an area effect since greater areas with lots of filaments could be better targets for parasites. A greater heterogeneity of gills is surely by implication of a greater area but it is difficult to escape the circular argument. The structural complexity of gill environments is clearly too important to be neglected in studies of parasite ecology. More emphasis should be given to research on habitat

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heterogeneity in gill systems of fish (Guégan and Hugueny, unpublished work). In our case, studies investigating the exact proportion between fish body size and total gill area, which is generally strong in Paleartic freshwater fish (Wootton 1990), could demonstrate the effect of gill surface area on larval recruitment by monogeneans. Unfortunately, these data are virtually nonexistent since we were principally interested in fish body length data in the field in West Africa.

Extinction-capture phenomenon

Price (1987) has proposed an "asymptotic equilibrium model" describing an equilibrium of parasite communities resulting from a balance between parasite colonizations and extinctions. Parasite extinctions are assumed to be due to a combination of factors such as intra- or interspecific competition as well as various stochastic events.

Guégan and Agnèse (1991) demonstrated large parasite captures in cyprinids. The species *L. coubie* behaves as a source of parasite transmission. *L. roseopunctatus, L. parvus* and *B. bynni* are sensitive to this parasite invasion (Guégan and Agnèse 1991). *L. obscurus* which is the sister-species of *L. parvus* is not affected by these transfers, since it is not sympatric (sometimes parapatric) with *L. coubie* (Guégan and Lambert 1991; Guégan and Agnèse 1991).

The outcome of monogenean extinction and colonization is that three species of *Dactylogyrus* have disappeared in *L. parvus*, whereas only one species has colonized it. This apparent imbalance is probably compensated by greater density of parasite populations on *L. parvus*, as reported in other groups of animals by Faeth (1984). Captured *Dactylogyrus* undergo a population explosion on the gills of *L. parvus* (Guégan 1990).

Another interesting example of extinction/colonization is that of the monogeneans of *Barbus bynni occidentalis* and *B. petitjeani*. A recent contact between the two cyprinid species, has resulted in an exchange of their gill parasites. All the monogenean species of *B. bynni occidentalis* can be found on the gills of *B. petitjeani* whereas the opposite situation is never the case. Parasites specific to *B. petitjeani* tend to disappear due to the effects of invasion and are replaced by the new invader forms. This amounts to a displacement of parasite fauna analogous to the "turnover" observed in animal groups on islands (Roughgarden 1986), i.e. new species are recruited, which drive away resident species.

To summarize, it appears that there is a turnover of the gill parasite fauna in cyprinids, whose mechanism is a combined process of parasite extinction and colonization. However, it is difficult to demonstrate dynamic equilibrium resulting from a balance between parasite extinction and colonization as in studies dealing with insular biogeography (Simberloff 1976; Abbott 1983).

Historical factors

Parasite community construction is not only the result of probability and/or independent extinction-colonization processes. It is also the final consequence of a long coevolution between species that will build together functional networks. The history of host-parasite relationships is an essential element to consider in analyzing the structure of parasite communities (Brooks 1980, 1988). When related host species cohabit an environment, exchanges of parasites can occur. In general, nonspecialized parasite species must have more successful invaders than overspecialized species (Combes 1990). The shift in parasite colonization eventually disturbs the older parasite structure. Inversely, when host fish species remain isolated for a long time in drainage basins that are themselves isolated (Hugueny 1989a, b), their parasites can be considered to result directly from host-parasite cospeciation (Brooks and Bandoni 1988). Most genera of west African cyprinids have distinct groups of monogeneans which are probably the result of a long association between hosts and parasites (Guégan and Agnèse 1991).

Hypothesis of refuge areas

In a study of fish communities in West Africa, Hugueny (1989a, b) determined three regions in which parasite species richness was greater than the value predicted by the model used. These three regions grossly correspond to three probable refuge areas for birds, butterflies, and mammals (Endler 1982; Mayr and O'Hara 1986), namely: (i) Liberia and Sierra Leone, (ii) Cameroon and Gabon, and (iii) Eastern Zaire. The present study is partially concerned with the first of these regions. The coexistence of phylogenetically related fishes, such as Guinean *Barbus* (Lévêque and Guégan 1990), may have facilitated lateral transfers of parasites and produced greater species richness than that predicted by our model. *Barbus sacratus, B. parawaldroni*, and *B. wurtzi* show high species richness (Fig. 1 see arrow) consisting of monogeneans of the same species (stenoxenic specificity) or monogeneans that are phylogenetically close (originating from host-to-host transfers followed by speciations).

To summarize, the coexistence of several related host species of freshwater fishes in the same drainage basin may have favored the maintenance of parasite species richness. It may also explain why the species richness exceeds that predicted by our model.

Conclusion

Greater interest is now being shown in parasite ecology not only by parasitologists (Esch et al. 1990; Rohde 1989) but also by researchers in other fields (Barbault 1988) who have discovered the usefulness of host-parasite systems in investigating factors structuring community constructions. All ecologists emphasize the difficulty or impossibility of determining the number of variables operating in a biotope. In a living environment,

individuals of a single host species regulate their relationships with the outside environment in the same manner, so that there may be fewer variables and their amplitude may be lower (Euzet 1989). Since host-parasite systems are often easier to understand than biotopes, they are good models for investigating evolutionary and ecological mechanisms that contribute to biological diversity (Rohde 1989).

In the present analysis of gill monogenean communities in west African cyprinid species, we propose an original approach to parasite species richness. The essential characteristics of the study are related to a unit system that comprises host species, parasite species, the fish gill apparatus, and biogeographical region.

The size of individuals of different species was found to be the main factor determining parasite species richness: the maximal size of the fish species accounted for 77% of monogenean species variability. The analysis of Price and Clancy (1983) showed that the range of host fishes was the most important factor influencing the number of parasite species per host. Rohde (1989) demonstrated that diversity of the host group could in some cases be an important factor determining species diversity of parasites. In our study, the ecology of the host species was the second factor: cyprinid species living in restrictive environments (turbulent waters, rapids) or near the surface (inaccessible to swimming parasite larvae) showed little or no parasitism.

Although many questions remain open, the present study at least determines the deciding factor of host species size and host species ecology for explaining monogenean species richness in West African cyprinid fishes. Animal size is undoubtedly the result of different adaptative pressures (Policansky 1983; Barbault 1990). They must be considered as central integrating characters in the evolution scheme, not only the product but also the source (i.e. parasite species richness) of variate adaptive pressures.

This initial approach is intended to stimulate discussions among parasitologists and promote further studies to elucidate the fascinating problems of parasite species richness.

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