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**A nested parasite species subset pattern in tropical fish:
host as major determinant of parasite infracommunity structure**

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Abstract The number of monogenean gill parasite species associated with fish hosts of different sizes is evaluated for 35 host individuals of the West African cyprinid *Labeo coubie*. The length of host individuals explains 86% of the total variation in monogenean species richness among individuals. Larger hosts harbour more species than smaller ones. The existence of a hierarchical association of parasite species in individuals of *L. coubie* is demonstrated. Monogenean infracommunities on larger fish hosts consist of all species found on smaller hosts plus those restricted to the larger size categories, suggesting some degree of compositional persistence among host individuals. The findings provide strong support for an interpretation of the relationship between monogenean parasite species richness and host body size in terms of a nested species subset pattern, thus providing a new record of repetitive structure and predictability for parasite infracommunities of hosts.

Key words Africa · Parasite species richness
Freshwater fish · Community ecology
Nested subset pattern

Introduction

Hosts, defined as home, mating point and resource for parasites, consist of replicated habitats in time and space. Host-parasite systems are undoubtedly interesting models for understanding patterns and processes in community ecology (Price 1990). For instance, recent studies have addressed the question of whether helminth communities

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are random aggregations of species, or structured repetitive organisations and thus predictable (Bush 1990; Thoney 1993). Moreover, and despite numerous surveys and the large quantity of data available to us, parasite community ecology needs more studies at the infracommunity level (Kennedy 1990). In this paper, we use the specific terminology adopted by Bush and Holmes (1986): the infrapopulation is defined as all members of a parasite species within a single host, the infracommunity refers to all the infrapopulations within an individual host.

Rich parasite communities were found in fish of tropical biomes (Rohde 1982), with up to 13 monogenean species present on a single fish host from West Africa (Guégan et al. 1992). Guégan et al. (1992) found a positive relationship between maximal host body size and the maximal individual monogenean species richness of hosts for 19 West African cyprinid fish species. We attempt to explain here whether or not monogenean species richness at the infracommunity level can be predicted. Monogeneans are hermaphrodite helminth parasites with a direct life cycle and a short free-living stage. In most monogeneans, the eggs leave the host and develop on or in the bottom sediment (Kearn 1986). A ciliated larva hatches from the egg and infects another host-fish individual. It is this ciliated larva that has the task of finding the fish host. Contact transfer of mature worms and development of larvae without leaving the host can occasionally happen but it is very limited, according to Baër and Euzet (1961), and only three successive parasite generations would occur on one host individual among *Dactylogyrus* species. Moreover, *Dactylogyrus* species on the gills of European freshwater fish can live for 2–3 months (Zharikova and Izyumova 1990). This suggests that the pattern in parasite community structure that we observed cannot be associated with the method of reproduction by worms, and the age structure of parasite populations. In addition, monogeneans are considered to have little pathological impact on host viability, except in some particular cases, such as captivity.

Kuris et al. (1980) considered hosts as biological islands at three different levels: host individual, host popu-

lation and host species. It is the first level that will be considered in this study which examines the helminth infracommunity structure in different fish-host individuals of the Western African cyprinid *Labeo coubie*. The host population is considered to be an archipelago with each host individual representing a separate island. Is there a positive relationship between host body size and infracommunity parasite species richness? Many investigators (Dogiel 1964; Price 1977; Lawton and Price 1979; Bell and Burt 1991) have shown that host size, or/and age, does have an effect on parasite communities, since larger hosts are also older and have been exposed to parasite colonisation for a longer period. Moreover, as fish body size increases, the gill surface area increases, thus permitting a larger number of parasites to infect hosts. Does this increase of parasite species richness occur at random, or is there a predictable pattern of parasite infracommunity structure? Generally, the commonest departure from an independent assortment of free-living species among islands is the nested subset pattern (Patterson and Atmar 1986; Patterson 1990), in which the species comprising a depauperate fauna constitute a proper subset of those in richer faunas. Our results are considered and discussed in comparison to the above model, the predictions of which are often observed in free-living animal communities on islands.

Material and methods

Data

L. coubie Rüppell 1832 is both the largest and the most widely distributed cyprinid in West Africa (Lévêque et al. 1990). Forty-nine fish collected with gill-nets all over West Africa [among them 35 specimens caught in two drainage basins: the Niger at Bamako in Mali (28 individuals), and the Upper Senegal in the Baoulé River in Mali (7 individuals)] were analysed. High affinities of fish communities (Daget 1954; Poll 1973; Paugy et al. 1990) between the Senegal and Niger basins in general, genetical (Guégan and Agnès 1991) and parasitological (Guégan et al. 1988, 1989) similarities between populations of *L. coubie* in particular, and recent connections during the Late Quaternary between the Baoulé and Niger Rivers (Grove 1985) justified the combination of samples from these two rivers. For each 1 of the 35 host individuals, 3 distinct variables were measured (Table 1): standard length (SL) of fish from the snout to the start of the caudal fin, species richness (SR) of monogenean species found within a single host individual, and presence/absence (+/-) of each monogenean species in a host individual. The code for the 13 monogenean species is as follows: 1, *Dactylogyrus digitalis*; 2, *Dactylogyrus retroversus*; 3, *Dogielius clavipenis*; 4, *Dogielius anthocolpos*; 5, *Dogielius flagellatus*; 6, *Dactylogyrus* sp. (this monogenean species was too scarce to allow a valid description); 7, *Dogielius complicitus*; 8, *Dactylogyrus falcilocus*; 9, *Dactylogyrus titus*; 10, *Dogielius harpagatus*; 11, *Dactylogyrus oligospirophallus*; 12, *Dactylogyrus jaculus*; 13, *Dactylogyrus decaspirus*. Descriptions of parasite species are taken from previous works (Guégan et al. 1988, 1989), except for one monogenean species (see above). All monogenean helminths of *L. coubie* are strictly confined to this host species (Paugy et al. 1990; Guégan and Agnès 1991).

Statistical methods

Standard linear least-squares regression techniques and correlation coefficients were used to analyse the different relationships

Table 1 Locality, standard length (SL) and species richness (SR) in monogeneans, and presence/absence (+/-) of 13 monogenean species (coded 1-13: see text) for 35 host individuals of the West African cyprinid fish *Labeo coubie*.

No. of fish	River	SL (mm)	SR	+/-
1	Niger	365	9	1, 3, 4, 8, 9, 10, 11, 12, 13
2	Niger	195	2	1, 2
3	Niger	253	3	1, 2, 4
4	Niger	100	0	-
5	Niger	115	3	1, 4, 11
6	Niger	250	6	1, 2, 4, 8, 9, 11
7	Niger	162	4	1, 2, 4, 9
8	Niger	236	4	1, 2, 4, 9
9	Niger	235	5	1, 2, 4, 9, 10
10	Niger	290	8	1, 3, 4, 8, 9, 10, 11, 12
11	Niger	310	8	1, 3, 4, 8, 9, 10, 11, 12
12	Niger	180	3	1, 9, 10
13	Niger	185	3	1, 2, 3
14	Niger	185	5	1, 2, 4, 8, 11
15	Niger	150	4	1, 8, 9, 10
16	Niger	155	3	1, 3, 12
17	Niger	120	2	1, 4
18	Niger	125	1	1
19	Niger	160	2	1, 9
20	Niger	170	2	1, 2
21	Niger	175	3	1, 4, 8
22	Niger	180	1	1
23	Niger	185	1	1
24	Niger	110	0	-
25	Niger	115	0	-
26	Niger	135	0	-
27	Niger	150	0	-
28	Niger	155	0	-
29	Baoulé	105	0	-
30	Baoulé	135	0	-
31	Baoulé	180	4	1, 3, 4, 8
32	Baoulé	253	4	1, 2, 3, 12
33	Baoulé	305	7	1, 2, 4, 8, 9, 11, 12
34	Baoulé	447	10	1-4, 8-13
35	Baoulé	497	13	1-13

(Dagnélie 1988). Untransformed, exponential and power function models were fitted to the relationship between host body length and monogenean species richness, and the model that adequately linearised the relationship and reduced the variation of points around the regression line was accepted as the best model (Connor and McCoy 1979). We used a $\ln(x+1)$ transformation for parasite species richness.

The association of monogenean species on particular host individuals and the existence of a nested subset pattern was examined using the index of nestedness (N) described by Patterson and Atmar (1986). This index is the sum of instances where a species is absent from a richer host than the most depauperate one on which it occurs. If the matrix is perfectly nested, N is zero and N grows larger as nestedness diminishes. In order to test the statistical significance of the observed nestedness in the assemblage, Patterson and Atmar (1986) proposed to compare it with the expected value under the hypothesis of random allocation of species on sites (here on host individuals). For this purpose, they developed two computer programs, RANDOM0 and RANDOM1. In the former, each species has the same probability of being chosen when simulated assemblages are constituted; in the latter, probability of choice is proportional to the observed occurrence (here number of parasitised host individuals for each monogenean species). In both, parasite species are chosen until the number of simulated parasite species on each individual host matches the observed value number. We used these two programs and assessed the statistical significance of the results in the following way. We generated 1000

random presence-absence matrices and counted how many times simulated values of N were less than, or equal to, the observed value. Dividing this value by the number of simulations gives the statistical significance of the observed nestedness, as estimated by the randomisation procedure (Patterson and Atmar 1986).

Results

Table 2 summarises the different relationships between infracommunity parasite species richness and host individual length. The best fit shows a simple linear relationship of parasite species richness versus host individual length (Fig. 1). No trends were present in the residual values. The length of host individuals accounts for 86% of the total variation in monogenean richness. No parasites were collected from fish less than 115 mm in length.

In order to determine whether there exists a hierarchical association of parasite species in relation to host individual length, 27 fish specimens (those for which the parasite richness was superior to 0), and 13 monogenean species were analysed. Our records provide data suitable

Table 2 Relationships (simple, semi-logarithmic and logarithmic transformations), between monogenean species richness (SR) and length of host individuals (SL) (r =correlation coefficient).

Variables	Intercept	Slope	r	P
SR-SL	-3.00	0.43	0.921	0.0001
SR-lnSL	-34.34	7.24	0.901	0.0001
lnSR-SL	-0.15	0.33	0.781	0.0001
lnSR-lnSL	-7.41	1.65	0.821	0.0001

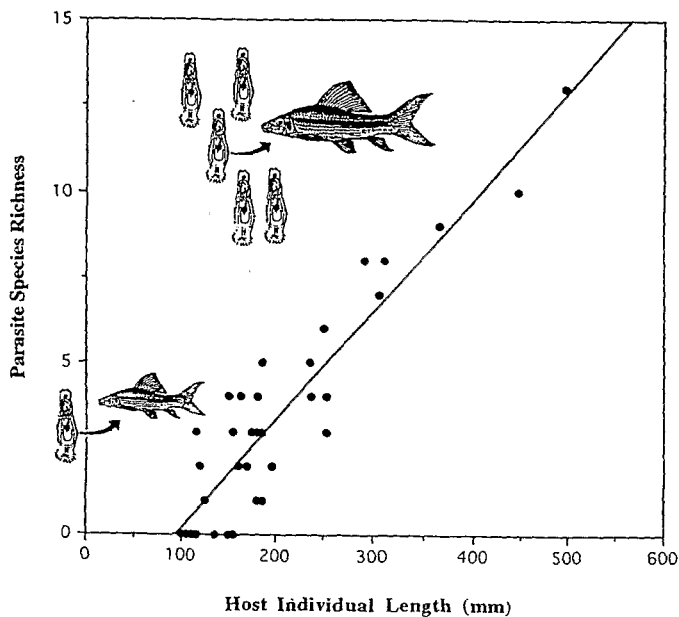


Fig. 1 Relationship between monogenean species richness and host-individual length (mm) for 35 fish individuals of the West African cyprinid species *Labeo coubie*.

for an analysis of a nested species subset since the total number of islands examined for free-living organisms is usually much smaller than 27. The resulting nestedness index is $N = 85$, which is highly significant ($P < 0.001$), regardless of the program used. Consequently, monogenean species are not distributed at random in their hosts. Larger host individuals having higher parasite species richness carry parasite species which are rarely found in smaller hosts having few monogenean species.

Discussion

Our results show a general pattern of enrichment of gill parasite species with host individual length and/or age of *L. coubie*. This follows a nested subset pattern, a phenomenon also described as an hierarchical association by Cornell (1986) for free-living organisms, or an accumulation of species by Rohde (1979) for parasites. The existence of a nested subset pattern allows us to rank parasites along a species gradient, i.e. from species found only in fish hosts harbouring rich parasite communities (high- S species sensu Diamond 1975) to species present in all hosts (indifferent species). There are two hypotheses which can be used to explain the increase of parasite species richness with individual host body size. The first corresponds to the effect on passive sampling of parasite species of an increase in gill surface area: greater host body size implies a greater gill surface area which is interpreted to mean greater randomly occurring parasite richness in fish. The second represents the effect on passive sampling of parasite species of fish age: as fish become older, the length of time a host has been available for random parasite colonisation increases. Under the passive sampling hypothesis, the common species are expected to be found on many fish and the rare species restricted to individuals which have 'sampled' parasites for the longest time (i.e. the oldest individuals) or most intensively (i.e. the largest individuals). A positive relationship between occurrence and mean local (per host) abundance is also expected (Wright 1991). As the RANDOM1 model weights the probability of a parasite species being chosen by its occurrence it can be considered that this model mimics roughly, if not perfectly, a passive sampling hypothesis process. Considering that the RANDOM1 model doesn't agree with our data, the observed pattern is unlikely to be the result of a passive sampling process. However, in order to reject this hypothesis unambiguously it is necessary to have information about parasite population size (Coleman et al. 1982). Patterson and Atmar (1986) consider the nested subset pattern to be the result of two main processes. The first of these represents a selective extinction of species in relation to their density. The second represents differential colonisation capabilities: remote islands are inhabited only by species having good dispersal capabilities, whilst islands close to sources of colonists are inhabited by poor and good dispersers. In our case, this latter hypothesis can be discarded because of the simple fact that each individual

host is a colonising source for all other hosts and no distinction can be made between 'remote' and 'close' host islands. Our primary objective is to discuss the main biological reasons and ecological concepts that can account for the parasite community changes observed.

Gill habitat heterogeneity hypothesis

The habitat heterogeneity hypothesis postulates that the larger the surface of an island, the more types of habitat it will contain, thus increasing species richness (Connor and McCoy 1979). For gill ectoparasites, this hypothesis assumes that the gill surface area will be more diversified on larger fish than on smaller fish. It is also assumed that the gill habitats present in smaller hosts are still present in larger hosts, which thus display a nested subset pattern. Several studies provide evidence for the diversification of gill habitats. Silan et al. (1987) and Buchman (1991) have shown that larger bass and eel, harbour a greater and more diversified surface respectively to which monogenean larvae may attach. Similar results have been found for copepodids of the American brook trout (Poulin et al. 1991). In fact, the gill area changes in different ways (Wootton 1990), and some studies underline its importance for parasite assemblages (see Rohde 1979, 1989 for a review). Monogeneans may partition their gill habitat by morphological differentiation in anchors. Pugachev (1988) has addressed the fundamental functional morphology of these worms, and has shown that the attachment mechanisms used by these helminths are diverse in their mode of action. We recognized two kinds of morphological differentiation among the monogenean species studied (Fig. 2a). However, we were unable to link statistically, either anchor size or an-

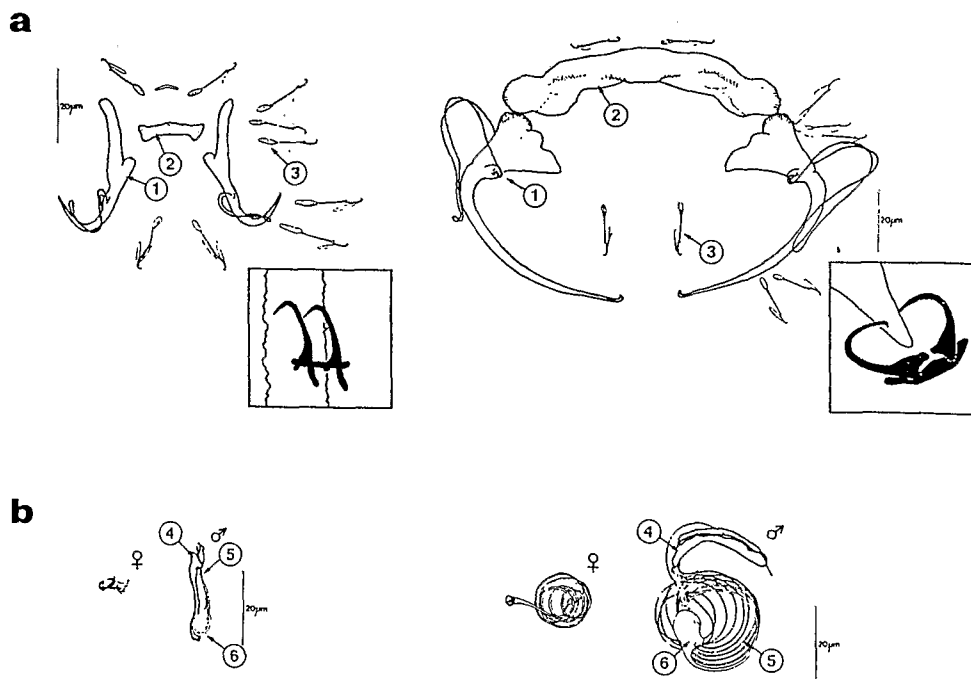
chor type to the position occupied by the different monogenean species along the indifferent to high-*S* species gradient. Most of the recent information regarding gill habitat heterogeneity reveals an increasing complexity in space and time, but few studies have been devoted to demonstrating that the addition of 'new' gill habitats resulting from fish growth arises without the disappearance of 'old' gill habitats, a condition necessary for the nested subset patterns observed here.

Hypothesis of density-dependent extinction rates

Many models of free-living organisms on islands show that the probability of population extinction increases when population size decreases (Richter-Dyn and Goel 1972; Leigh 1981; Schaffer and Samson 1985; Pimm et al. 1988). These population properties are intimately associated with the existence of a nested subset pattern (Patterson and Atmar 1986; Bolger et al. 1991). Only species able to reach high densities will have no risk of extinction on small islands, and they will be able to colonise a wide range of islands. In contrast, species which are unable to reach high densities are restricted to large islands where they can attain a sufficient population size to prevent extinction. Such a scenario is expected under the assumption of a very limited or non-existent exchange of propagules between infrapopulations, and implies the absence of a rescue effect (Brown and Kodric-Brown 1977). For parasites, the composition of their assemblage in hosts presumably depends on the size of infrapopulations capable of settling on host individuals of different size ranges (Dobson 1990). Unlike free-living populations on islands, however, monogenean life cycles display high immigration rates between

Fig. 2 a Morphological differentiation of monogenean anchors: genus *Dactylogyrus* (on the left), genus *Dogielius* (on the right). Figures in boxes show the way in which worms hatch on secondary gill filaments.

b Female and male sexual apparatus of monogenean species. The vagina consist of a more or less sclerotised pocket not prolonged (on the left) or prolonged (on the right) by a hollow tube, and an external pore. Male copulatory apparatus consists of a basic ampulla followed by a fine, short penis which may be linear (on the left), or form a single spiral (on the right), and a sclerotised bifid accessory piece in which the penis slides (after Guégan et al. 1988, 1989). There is no taxonomic link between a and b (1 hamulus, 2 transversal bar, 3 marginal hooklet, 4 accessory piece, 5 penis, 6 basal ampulla



host individuals via their larvae. Therefore monogenean infrapopulations are very different from free-living populations on true islands, and the population models listed above cannot be applied to monogenean parasites. Gill parasite infrapopulations can instead be considered as belonging to a parasite metapopulation that includes all infrapopulations among host individuals. Hence, extinction rates in monogenean communities must be considered in a metapopulation context, in which extinction in an individual host is compensated for by the immigration of parasites from other host individuals. *De facto*, there is little evidence to support the hypothesis of density-dependent extinction rates resulting in a nested subset pattern, unless parasite species have similar between-host immigration rates.

Hypothesis of positive parasite interactions

Observation of helminth communities in snails shows that some trematode species are found only in hosts harbouring a previous infection of another trematode species (Kuris 1990). This is because one parasite species depresses the host immune system, thereby enhancing colonisation and/or reproduction of other species. Although multiple infections are often observed in monogenean gill parasites (Euzet and Combes 1980), there is no strong evidence that positive interactions influence monoxenous ectoparasite communities in fish. Such an effect could generate a nested pattern of colonisation but more work is required to establish whether such a hypothesis is plausible.

Hypothesis of host-habitat relationships

Host diet, foraging strategies and habitat diversity are the three most basic factors affecting parasite communities in hosts. Generally, large fish have higher dispersal abilities than small fish, both within and between species. As fish size increases, individuals may be expected to use more diverse habitats, and to forage in a wider range of places. Habitats of young and adult *L. coubie* can differ in depth, habitat topography, relationship to prevailing currents and other features which considerably influence parasite infestation and composition. Lauzanne (1988) observed that younger *L. coubie* live in prevailing currents whereas adults prefer quiet waters. Guégan et al. (1992) demonstrated that rheophilic cyprinid species do harbour a lower gill parasite richness than all other cyprinids analysed. This suggests that high current velocity may prevent parasites from colonising potential hosts. Intuitively, parasite species found only on larger host individuals could correspond to species unable to reach young fish hosts living in habitats with strong currents. This tentative scenario underlines the role of the host ontogenetic niche shifts as an explanation for differences in parasite composition among host individuals of different age and size in *L. coubie*.

Conclusion

The cogent contribution of Kennedy et al. (1986) identified host characters which determine the resource base of parasites, and therefore act as major factors contributing to the parasite community. In this work, we provide strong evidence that individual host size in fish can explain the monogenean species richness observed among 35 individuals of the West African freshwater cyprinid *L. coubie*. Greater gill-parasite species-richness was observed in fish with a greater gill surface area. Four general hypotheses, none of which are mutually exclusive, were composed to account for observations made on parasite community structure: (1) increase in gill habitat heterogeneity with host size and/or age, (2) increase in the extinction rates among parasite infrapopulations on the smallest host individuals, (3) positive parasite interactions, and (4) host ontogenetic niche shift.

The development of large infrapopulations of high-S parasite species in the largest hosts offsets the cost of colonising hosts which exist at low density, indicating that host individuals with a high mortality rate (largest and/or oldest individuals) considerably influence parasite population dynamics. Personal observations (J.F. Guégan 1990) show that some high-S monogenean species have developed life strategies which would permit self-fertilisation, whereas the general strategy among monogeneans is cross-fertilisation (Fig. 2b). To consider the nested subset pattern as a general pattern among monogenean communities in fish, comparative studies between high-S and indifferent parasite species will need more specific attention. Data on *L. coubie* clearly demonstrate that host biology determines parasite community structure and influences considerably the *cortège* of parasites available to it. Central to this scheme is the integrating character of host body size, which overshadows other unpredictable variables in contributing to the evolution of parasite communities.

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References

- Baër JG, Euzet L (1961) Classe des Monogènes. In: Grassé PP (ed) *Traité de Zoologie*, vol 4. Masson, Paris, pp 243–325
- Bell G, Burt A (1991) The comparative biology of parasite species diversity: intestinal helminths of freshwater fishes. *J Anim Ecol* 60: 1046–1063
- Bolger DT, Alberts AC, Soulé ME (1991) Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. *Am Nat* 137: 155–166
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58: 445–449
- Buchman K (1991) Relationship between host size of *Anguilla anguilla* and the infection level of the monogeneans *Pseudodactylogyrus* spp. *J Fish Biol* 35: 599–601
- Bush AO (1990) Helminth communities in avian hosts: determinants of pattern. In: Esch G, Bush A, Aho J (eds) *Parasite*

- communities: patterns and processes. Chapman and Hall, London New York, pp 197-232
- Bush AO, Holmes JC (1986) Intestinal parasites of lesser scaup ducks: patterns of association. *Can J Zool* 64: 132-141
- Coleman BD, Mares MA, Willig MR, Hsieh YH (1982) Randomness, area, and species richness. *Ecology* 63: 1121-1133
- Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. *Am Nat* 113: 791-833
- Cornell HV (1986) Oak species attributes and host size influence cynipine wasp species richness. *Ecology* 67: 1582-1592
- Daget J (1954) Les poissons du Niger supérieur. *Mém de l'I.F.A.N.* 36: 1-391
- Dagnélie P (1988) *Théorie et méthodes statistiques*, vol. I. Les Presses Agronomiques de Gembloux, ASBL, Gembloux
- Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. Harvard University Press, Harvard, pp 342-444
- Dobson AP (1990) Models for multi-species parasite-host communities. In: Esch G, Bush A, Aho J (eds) *Parasite communities: patterns and processes*. Chapman and Hall, London New York, pp 261-288
- Dogiel VA (1964) *General parasitology*. Oliver and Boyd, London
- Euzet L, Combes C (1980) Les problèmes de l'espèce chez les animaux parasites. In: *Les problèmes de l'espèce dans le règne animal*. *Mém Soc Zool Fr* 3: 239-285
- Grove AT (1985) The physical evolution of the river basins. In: Grove AT (ed) *The Niger and its neighbours*. Environmental history and hydrobiology, human use and health hazards of the major West African rivers. Balkema, Amsterdam, pp 21-61
- Guégan JF (1990) Structure des peuplements parasitaires: le modèle Monogènes de Cyprinidae ouest-africains. Doctoral thesis, University of Montpellier II, Montpellier, France
- Guégan JF, Agnèse JF (1991) Parasite phylogeny events inferred from host phylogeny: the case of monogenean gill parasites of *Labeo* (Teleostei, Cyprinidae). *Can J Zool* 69: 595-603
- Guégan JF, Lambert A, Euzet L (1988) Etude des Monogènes de Cyprinidae du genre *Labeo* en Afrique de l'Ouest. I: Genre *Dactylogyrus* Diesing, 1850. *Rev Hydrobiol Trop* 21: 135-151
- Guégan JF, Lambert A, Euzet L (1989) Etude des Monogènes de Cyprinidae du genre *Labeo* en Afrique de l'Ouest. -I: genre *Dogielius* Bykhowsky, 1936. *Rev Hydrobiol trop* 22: 35-48
- Guégan JF, Lambert A, Lévêque C, Combes C, Euzet L (1992) Can host body size explain the parasite species richness in tropical freshwater fishes? *Oecologia* 90: 197-204
- Kearn GC (1986) Role of chemical substances from fish hosts in hatching and host-finding in monogeneans. *J Chem Ecol* 12: 1651-1658
- Kennedy CR (1990) Helminth communities in freshwater fish: structured communities or stochastic assemblages? In: Esch G, Bush A, Aho J (eds) *Parasite communities: patterns and processes*. Chapman and Hall, London New York, pp 131-156
- Kennedy CR, Bush AO, Aho JM (1986) Patterns in helminth communities: why are birds and fish different? *Parasitology* 93: 205-215
- Kuris AM (1990) Guild structure of larval trematodes in molluscan hosts: prevalence, dominance and significance of competition. In: Esch G, Bush A, Aho J (eds) *Parasite communities: patterns and processes*. Chapman and Hall, London, New York, pp 69-100
- Kuris AM, Blaunstein AR, Alio JJ (1980) Host as islands. *Am Nat* 116: 570-586
- Lauzanne L (1988) Les habitudes élémentaires des poissons d'eau douce africains. In: Lévêque C, Bruton MN, Ssentongo GW (eds) *Biologie et écologie des poissons d'eau douce africains*. ORSTOM, Paris, pp 221-242
- Lawton JH, Price PW (1979) Species richness of parasites on hosts: agromyzid flies on the British Umbelliferae. *J Anim Ecol* 48: 619-637
- Leigh EG (1981) The average life time of a population in a varying environment. *J Theor Biol* 90: 213-239
- Lévêque C, Paugy D, Teugels GG (1990) *Faune des Poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest*, vol I. ORSTOM, Collection Faune tropicale, Paris
- Patterson BD (1990) On the temporal development of nested subset patterns of species composition. *Oikos* 59: 330-342
- Patterson BD, Atmar W (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol J Linn Soc* 28: 65-82
- Paugy D, Guégan JF, Agnèse JF (1990) Three simultaneous and independent approaches to the characterization of a new species of *Labeo* (Teleostei, Cyprinidae) from West Africa. *Can J Zool* 68: 1124-1131
- Pimm SL, Jones HL, Diamond JM (1988) On the risk of extinction. *Am Nat* 132: 757-785
- Poll M (1973) Nombre et distribution géographique des Poissons d'eau douce africains. *Bull Mus natn Hist nat*, Paris 150: 113-128
- Poulin R, Curtis MA, Rau ME (1991) Size, behaviour, and acquisition of ectoparasitic copepods by brook trout *Salvelinus fontinalis*. *Oikos* 61: 169-174
- Price PW (1977) General concepts on the evolutionary biology of parasites. *Evolution* 31: 405-420
- Price PW (1990) Host populations as resource defining parasite community organization. In: Esch G, Bush A, Aho J (eds) *Parasite communities: patterns and processes*. Chapman and Hall, London New York, pp 21-40
- Pugachev ON (1988) Principles of the functional morphology analysis of the lower monogene anchors (in Russian, English abstract). In: Bauer ON, Pugachev ON (eds) *Monogenea investigations*. USSR Academy of Sciences, Proc Zool Inst Leningrad 117: 49-59
- Richter-Dyn N, Goel NS (1972) On the extinction of a colonising species. *Theor Popul Biol* 3: 406-433
- Rohde K (1979) A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. *Am Nat* 114: 648-671
- Rohde K (1982) *Ecology of marine parasites*. University of Queensland Press, St. Lucia, Queensland
- Rohde K (1989) Simple ecological systems, simple solutions to complex problems. *Evol Theor* 8: 305-350
- Schaffer ML, Samson FB (1985) Population size and extinction: a note on determining critical population size. *Am Nat* 125: 144-152
- Silan P, Euzet L, Maillard C, Cabral P (1987) Le Biotope des ectoparasites branchiaux de poissons: facteurs de variations dans le modèle Bars-Monogènes. *Bull Ecol* 18: 383-391
- Thoney DA (1993) Community ecology of the parasites of adult spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus* (Sciaenidae) in the Cape Hatteras region. *J Anim Ecol* 43: 781-804
- Wootton RJ (1990) *Ecology of teleost fishes*. Chapman and Hall, London New York
- Wright DH (1991) Correlations between distribution and abundance are expected by chance. *J Biogeogr* 18: 463-466
- Zharikova TI, and Izyumova NA (1990) Age structure of a population of *Dactylogyrus chraniilowi* (Monogenea), a parasite of the blue bream (*Abramis ballerus*). *Zool Zh* 69: 25-30