ENVIRONMENT AND HOST-PARASITE RELATIONSHIPS IN MONOGENEA

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Abstract. The interest of a new approach in taking up the problems of host-parasite relationships with environment is proposed in terms of population biology. Two different integrating levels are considered: a microenvironment that corresponds particularly to the host and a macroenvironment corresponding to the whole host-parasite system. Some examples are given that provide significant reasons in perceiving the biology of Monogenea under these aspects. To conclude we emphasize the importance of developing this new way for the study of hybrids models in relation to parental host systems.

Rohde (1982), who contributed significantly to the development of this subject, distinguished eight essential elements among the many dimensions of the **ecological niche**: host species, geographic distribution, macrohabitat, microhabitat, host sex and age, season and hyperparasitism.

The list is not restrictive, and this extreme division of the ecological niche does not appear to me to be useful in dealing concretely with these problems, since by definition the combination of all the interference among these factors constitutes the niche. In the context of host-parasite relationships, it is preferable to consider the environment on two different levels:

— a **microenvironment** that corresponds to the **host** and to the biotic and abiotic conditions it provides the monogeneans. This concerns the parasite phase of the cycle;

— a **macroenvironment** corresponding to the surroundings in general, in other words the environment of the whole **host-parasite system.** This concerns the free phase of the cycle as well as the parasite stage, since monogeneans are ectoparasites and the abiotic factors of their micro- and macroenvironments interfere with one another. Lastly, the influence of the macroenvironment on the host can in turn generate changes in the microenvironment, when the ecophysiological conditions change (migrations, reproduction periods, etc...). This distinction is of course artificial, but I consider it to be an important element in advancing the study of monogenean **population biology.** The concept of microenvironment in particular forms a basis for elucidating the **biotope** of these ectoparasites. The biotope has been found to be much more complex than what was initially assumed.

Let us consider first of all the **problems of monogenean microhabitat and localization.**

The hosts of monogeneans offer a wide range of specialized microhabitats. In the monocotylideans, for example, the "specificity" of localizations corresponds to the main taxonomic divisions: monocotylineans are generally branchial and dendromonocotylineans cutaneous, most of the merizocotylineans infest the olfactory organs, and calicotylineans show a clear tendency toward endoparasitism (cloaca, rectal gland, oviducts, coelom). Polystomatideans are vesical in the adult amphibian and branchial in the tadpole.

But the majority of monogeneans colonize the gill system. This is the substrate on which monopisthocotyleans and polyopisthocotyleans have so extremely diversi-

fied their fixation systems and means of attachment, which are the morphological aspects of diversity clearly observed by taxonomists. It is more difficult to demonstrate the biological diversity of monogeneans and thus to perceive all the ecological components that make fish gills the "showcase of current monogeneans". Varied parasite communities can be found on gills, involving several kinds of combinations (copepods, protozoa, etc...) and often, in the case of monogeneans, **simultaneous infestation by several congeneric species**. This type of infestation is particularly useful for studying ecological interactions of populations and their current dynamics, as well for speculating on the longer-term mechanisms of evolution in these systems.

In detailed studies, such as that of Silan et al. (1987) on the gill biotope of *Dicentrarchus labrax*, which harbors *Diplectanum aequans*, *D. laubieri* and *Serranocotyle labracis*, it can be seen that this biotope is in certain ways very heterogeneous. This author studied variations in the number of gill filaments and in the gill surface that could be colonized by the parasites during host growth. The results clearly show that apart from **heterogeneity, significant physical changes** occur in the gill biotope of these ectoparasites. Moreover, these changes take place rather quickly, considering their yearly amplitude. Since the changes are accompanied by abiotic variations related to the macroenvironment of the host-parasite system, the diversity of the gill biotope can only increase. The result is that a given stage of *Diplectanum* (juvenile or adult) is subject to different constraints depending on whether the filament is in a young or old host, and abiotic conditions are usually not identical in two host specimens with different ecophysiologies. Lastly, the differing behaviors of hosts in periods of growth or reproduction modify the parasite demographic data, via recruitment.

How are monogeneans distributed on such a heterogeneous substrate?

Rohde (1977), considers that ectoparasites living on fish gills show four main types of partitioning:
— transverse partitioning, revealing a preference for certain gill arches (type A),
— longitudinal partitioning, in which the parasites choose particular sector (type B),
— vertical partitioning, which corresponds to particular zones (type C),
— lateral partitioning, expressing a preference for external on internal hemibranchia (type D).

This list is not restrictive, and does not exclude the overlapping of partitioning types. This is one of the consequences of gill biotope heterogeneity. In *D. labrax*, for example, the partitioning of *Diplectanum* and *S. labracis* has been studied as a function of this heterogeneity, as well as variations in intensity (hence, the effects or density).

S. labracis satisfies the criteria for type A, B and D partitioning, but this is not the case of *D. aequans* and *D. laubieri*, which belong to none of the categories, or to all of them, depending on the method of integrating biotope variability and populations structure (taking into account stages and densities). The separate partitioning types can be analyzed as follows: (Silan 1984)
— **transverse partitioning**: spatial segregation occurs between *D. aequans* and *D. laubieri* when the biotope becomes larger and densities decrease. At a constant biotope size, it disappears as densities increase.

longitudinal partitioning: in small biotopes, *D. aequans* and *D. laubieri* occupy the same sectors (2 and 3), i.e. those most exposed to the respiratory current. *D. laubieri* preferentially occupies the more sheltered sectors (1 and 5) as hydrodynamic constraints increase with larger gill biotopes.
— **vertical partitioning**: this partitioning gradient is fundamental: it affects not only the monogenean species but also the **intraspecific age classes**. There is a centri-

fugal migration from the base of the filaments toward their extremity. Only the adults of *D. aequans* reach the distal zone and remain these. The young of *D. aequans* and the young and adults of *D. laubieri* remain withdrawn, which is even more the case when the biotope becomes larger. This restraint occurs even at the lowest intensities, and when individuals are isolated. Hence a local decrease in density resulting from an increase in gill size is not responsible for the intraspecific proximity of the young and adult stages of *D. laubieri*.
— lastly, **lateral partitioning** occurs mainly in large biotopes, where the anterior hemibranchia of arch I and the posterior hemibranchia of arch IV are the sites most infected by the two *Diplectanum*.

The colonization of the gill biotope has also been considered in terms of the arch gradient in sympatric and allopatric situations in *D. labrax*. When living sympatrically, *D. aequans* and *D. laubieri* colonize all the arches of young hosts, (with a slight preference for arches I and IV, evan at low density). *D. aequans* shows the same tendency on its own. On older hosts, i.e. with larger gill biotopes, a partitioning profile appears for each species (*D. aequans* on the anterior arches, *D. laubieri* on the posterior arches) although the densities have decreased. This profile persists at higher densities. In an allopatric situation, *D. aequans* retains its partitioning profile (decrease from arch I to IV).

These observations show that the separation of monogeneans along the arch gradient (i.e. one of the components of the spatial niche) does not in this case involve a competitive process.

The structural complexity of such environments should not be neglected in parasite ecology and host-parasite relationships. Gill heterogeneity inevitably has an influence on the structure of the colonizing populations and on that of everall infestation. This is an essential element that elucidates to some extent the **richness and species diversity** observed in a given environment as well as its short-and long-term development. Using the model of *D. aequans* and *D. laubieri*, Silan (1984) has shown that the **heterogeneity of the gill biotope allows constant readjustment of the niches** of these two monogeneans, which otherwise show significant biological differences (rate of development, growth, maturation, laying, etc...). In practical terms, this sort of study makes it possible to determine why one species, in this case *D. aequans*, causes pathological problems in fish farming, whereas *D. laubieri* always remains very unobstrusive.

The gill microenvironment, with its patchwork appearance, is of course influenced by the macroenvironment, i.e. the biotic and abiotic conditions of the environment that surrounds the host-parasite system. In this context, the model of simultaneous infestation by congeneric species takes on another dimension: it can be used to account for and determine **spatiotemporal variations in monogenean populations**, the variations in species diversity as a function of the environments and hosts.

Among the current problems related to these subjects are the following:
— in the **marine environment**, there are latitudinal gradients of species diversity and variations of the same kind as a function of depth (Rohde 1978, 1988). It is also known that species diversity is very wide in monogeneans of coral reefs. On this scale it is difficult to distinguish the contribution of biotic factors (for example, the diversity of hosts, whose role must be important, particularly with strictly and narrowly specific parasites) and abiotic factors in the influence of the macroenvironment on the gill biotope.

In **continental aquatic environments**, the greater amplitude of abiotic environmental factors (such as temperature) increases the heterogenity of gill biotopes. This must strongly condition the plurispecific parasitic variations described in many works

related to dactylogyrideans or gyrodactylideans (seasonal fluctuations, fluctuations as a function of host age, etc...) (Chubb 1977).

A new approach to investigating the significance of macroenvironmental factors could consist in comparing fluctuations of parasite populations under natural and artifical conditions (i. e., when hosts have been transferred to a different biogeo graphic region, to farming conditions, etc...). This would make it possible to see how the readjustment of niches occurs as a function of the environment:

— For example, North American centrarchideans introduced into Europe have a less diversified fauna than in their region of origin.

— The transfer of hosts, combined with farming conditons, can lead to drastic changes in parasites specificity compared to what is observed in the natural environment. This is the case of *Pseudodactylogyrus anguillae* of the European eel, which was found to be pathogenic for *Anguilla anguilla* in Japan (Ogawa and Egusa 1976).

— *Polylabris tubicirrus*, which in the Mediterranean only naturally infests sparideans of the genus *Diplodus*, produced massive infestations in *Sparus aurata* in the raceways of Corsica (Silan et al. 1985).

— Under other conditions, a parasite can considerably enlarge its natural biotope and invade other regions of the body. For example, *Benedenia monticelli* is strictly localized in the opercular folds of the mullet in the western Mediterranean, but it invades the body and caudal region in the eastern Mediterranean. (Paperna and Overstreet 1981).

These examples, which could all be multiplied, serve to show that host-parasite interactions with the environment must now be conceived in terms of **population biology**. The study of the structures and dynamics of monogenean populations in marine and fresh-water environments, and at the interfaces between these environments, is a priority for this group of Platyhelminthes, about which very little is quantitatively known. This approach, apart from its purely ecological aspects, is indispensable for elucidating the evolution of populations. For example, the model of *D. aequans* and *D. laubieri* can clarify certain forms of infestation, such as the strict monospecific infestation of *Lates niloticus* by *D. lacustris*. The host, a centropomidean (a family close to the serranideans) of marine origin, has only retained the most demographically generalized species in fresh water. Referring to our model, if *D. labrax* settled in fresh water, only *D. aequans* would be capable of colonizing the new environment.

Along the same lines, *Lucioperca lucioperca* must have originally harbored, along with the current *Ancyrocephalus paradoxus*, at least one other congeneric species: its extremely localized partitioning leaves considerable room in the gill biotope of the pike perch (all of arches I, II and III, and the anterior hemibranchia of IV). (Starovoitov 1986).

In contrast, certain models are more difficult to understand with respect to their "ongoing situation", such as in the case of a host with diversified and complex infestation (for example, *Brycinus nurse* in central Africa, with 8 species of *Annulotrema* and 3 of *Characidotrema*) which is found living sympatrically with closely related species that have only two or even one species of monogenean of the same genus (Birgi 1987). What factors, within the same macroenvironment, are responsible for the restriction of niches in certain hosts and their apparent saturation in others? Such models call for more detailed studies.

To conclude, I would like to emphasize this new way of perceiving host-parasite relationships with the environment. It consists in considering the host as the keystone of the system, as a true biological entity, by taking into account its **genetic variability**. Since the work of Bychowsky, observations of infestation in hybrid forms have tempered the concept of parasite specificity (Dupont and Crivelli 1988). However, to derive

explanations, the host and its monogeneans have to be studied in the same manner. The **hybrid model** has the advantage of being a recent system which offers parasites a **genetically original microenvironment**, compared to the parental species. Because of their behaviour or ecology, these hybrids can also colonize a **different macroenvironment**.

In such systems, narrowly specific monogeneans appear to be particularly attractive because of their potential for change, and in the work by Le Brun, we see the role played by hybrids in the conquest of new hosts for *Diplozoon gracile* (Le Brun et al. in press).

ЖИЗНЕННАЯ СРЕДА И ОТНОШЕНИЯ МЕЖДУ ХОЗЯИНОМ И ПАРАЗИТОМ В ГРУППЕ MONOGENEA

А. Ламберт

Резюме. Интерес к новому подходу к решению проблем отношений между хозяином и паразитом и жизненной средой заключается в терминах популяционной биологии. Выделяют два различных интегрирующих уровня: микроокружение, которое имеет отношение к хозяину и макроокружение, относящееся ко всей системе хозяин — паразит. Приведено несколько примеров приносящих весомые аргументы в пользу понимания биологии группы Monogenea с этой точки зрения. В заключении подчёркиваем значение разработки этого нового подхода для изучения гибридных моделей в отношении к родительским системам хозяев.

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THE SYSTEMATICAL COMPOSITION OF THE FAMILY HETERAXINIDAE AND OTHER ALLIED FAMILIES OF MONOGENEA

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Abstract. This paper briefly presents a system of Heteraxinidae and other allied small monogenean families of suborder Microcotylinea Lebedev, 1972 with the indication of specific composition of all taxa and diagnoses of some taxa; new families Megamicrocotylidae, Paramonoxinidae and Monaxinoididae are proposed.

In a previous paper (Mamaev 1986), the systematical composition of the family Microcotylidae was analysed. The present paper proceeds and follows the same pattern. (The reader is referred to the abovecited paper for introductory material, which also applies to this paper.)

Heteraxinidae (Unnithan, 1957) Price, 1962

Mazocraeidea, Microcotylinea. Haptor greatly asymmetric, seldom unilateral due to a reduction of clamps on the opposite side. Clamps are microcotylid type but with supplementary process trident or bident. Anchors frequently present and situated on the posterior end of haptor on the lappet. Buccal suckers usually aseptate. Intestinal limbs unfused, with lateral branches. Testes numerous, postovarial. Copulative apparatus is various. Ovary usually in form of interrogation mark. Vagina dorsal (double or single) or absent. True seminal receptacle present, rarely absent. Parasites of marine Perciformes (with few exceptions), mainly of Carangidae.

I. Heteraxininae Unnithan, 1957

Heteraxinidae with bilateral haptor on one side of which the clamps are more numerous and a little larger than on the other. Clamp skeleton is usually symmetric, consisting (as in Microcotylidae) of 5 sclerites but with trident or, rarely, bident processus medio-supplementarius. Anchors in adult absent, as a rule. Buccal suckers aseptate. Genital atrium armed or unarmed, seldom inconspicuous. Vagina usually mediodorsal, single but with two ducts; rarely there are two dorsolateral vaginae or completely absent. Parasites of Perciformes, mainly of Carangidae.

1. *Heteraxine* Yamaguti, 1938. Type (single) species: *H. heterocarca* (Goto, 1894) Yamaguti, 1938 (syn. *H. seriola* (Ishii, 1936) Yamaguti, 1938). Redescription — see Ogawa and Egusa (1977).

2. *Allencotyla* Price, 1962. Type species: *A. mcintoshi* Price, 1962. Other species: *A. pricei* Kritsky, Noble et Moser, 1978.

3. *Tripathiana* Unnithan, 1971. Type (single) species: *T. minuta* (Tripathi, 1959) Unnithan, 1971 (syn. *Heteraxine minuta* Tripathi, 1959).

4. *Heteraxinoides* Yamaguti, 1963. Type species: *H. triangularis* (Goto, 1894) Yamaguti, 1963. Other species: *H. argiropsi* Mamaev, 1977*; *H. atlanticus* Gayevska-

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* The species marked with asterisks were studied on the basis of collection materials.