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THE GILLS OF *Hemichromis fasciatus* PETERS, 1858 (TELEOSTEI, CICHLIDAE), A BIOTOPE FOR ECTOPARASITES : STRUCTURE, HETEROGENEITY AND GROWTH MODELS

Charles-Félix BILONG BILONG⁽¹⁾, Eve LE POMMELET⁽²⁾, Patrick SILAN^{(2)*}

⁽¹⁾ Laboratoire de Biologie Générale, Faculté des Sciences, Université de Yaoundé I, BP. 812 Yaoundé, Cameroun.

⁽²⁾ CNRS (UPR 9060), Station Méditerranéenne de l'Environnement Littoral, Université Montpellier II, 1 Quai de la Daurade, 34200 Sète, France (e-mail : silan@univ-montp2.fr)

SUMMARY

(original scientific paper)

Fish gills constitute an heterogeneous biotope for many ectoparasite communities. Their modifications during fish maturation are partly at the origin of this heterogeneity. The number of gill filaments and the gill area colonizable by ectoparasites generally increase with the fish age. For *Hemichromis fasciatus*, an african Cichlidae (Teleostei), this increase of filament number can be fitted by an exponential model, and the colonizable area growth by a polynomial function. These models are compared with those of two temperate teleosts already known.

KEY WORDS: *Hemichromis fasciatus* - Gills - Biotope - Structure - Growth models - Parasite ecology.

RÉSUMÉ

(article original)

LES BRANCHIES D'*HEMICHROMIS FASCIATUS* PETERS, 1858 (TELEOSTEI, CICHLIDAE), UN BIOTOPE POUR DES ECTOPARASITES : STRUCTURE, HÉTÉROGÉNÉITÉ ET MODELES DE CROISSANCE.

Les branchies des poissons constituent un biotope hétérogène pour de nombreuses communautés d'ectoparasites. Leurs modifications au cours de la croissance des poissons sont en partie à l'origine de cette hétérogénéité. Le nombre de filaments branchiaux et la surface branchiale colonisée par les ectoparasites augmentent généralement avec l'âge du poisson. Pour *Hemichromis fasciatus*, un Cichlidae africain (Teleostei), l'augmentation du nombre de filaments peut être décrit par un modèle exponentiel, et la croissance de la surface branchiale colonisable par une fonction polynomiale. Ces modèles sont comparés avec ceux, connus, de deux téléostéens des milieux tempérés.

MOTS CLÉS : *Hemichromis fasciatus* - Branchies - Biotope - Structure - Modèles de croissance - Écologie parasitaire.

INTRODUCTION

Host-parasite systems allow interesting approaches for studying spatial structures in these animal communities. Any organ of a host, if colonized by several parasites, can constitute a biotope for a parasite community. At the host individual level, this biotope is termed "elementary" (SILAN *et al.*, 1987). The reproductibility of these units allows comparative studies of homologue communities, or guilds if the species are taxonomically and ecologically close. A precise knowledge of this biotope is necessary to study its functional structure. The heterogeneity of the gill biotope has been underlined (SILAN *et al.*, 1987; ROUBAL,

1987; SILAN & LE POMMELET, 1995; CALTRAN & SILAN, 1996). This heterogeneity is associated with external environmental factors (abiotic parameters of the aquatic environment, hydrodynamism...) and on the other, with the structure of host gills: number and shape of gill filaments, colonizable gill area. The amount of available resources and the nature of environmental constraints depend on the size and structure of this biotope.

Hemichromis fasciatus PETERS, 1858, an african Cichlidae (Teleostei), is parasitized by eight species of Ancyrocephalidae (Monogenea) (BILONG BILONG & EUZET, 1995). These ectoparasites coexist on gills and share the different resources (food, space...) of this

*Author to whom correspondence should be addressed.

biotope. Changes in gill structure in relation with the host maturation are hereby studied. The results are compared with those already obtained by SILAN *et al.* (1987) for *Dicentrarchus labrax* (LINNÉ, 1758) (Moronidae), then CALTRAN & SILAN (1996) for *Liza ramada* (RISSO, 1826) (Mugilidae).

MATERIAL AND METHODS

99 *Hemichromis fasciatus* were caught in the Yaounde municipal lake (Cameroon) using a fishing-net. After their capture, they were immediately immersed in either a solu-

tion of alcohol 70° or formoline 10%, and then stored in the same medium. The standard lengths of fish individuals are between 16 and 155 millimeters.

Gill filaments of each hemibranch of the four unilateral gill arches were counted under a dissecting microscope. Left and right arches were indiscriminately considered because of their symmetry. Arch I is the most anterior and arch IV the most posterior in the head-tail direction.

Colonizable gill area was measured according to SILAN *et al.* (1987), but this biological model requires to consider all hemibranches. Curve fitting using maximum likelihood and computations have been carried out with MLP (ROSS, 1980).

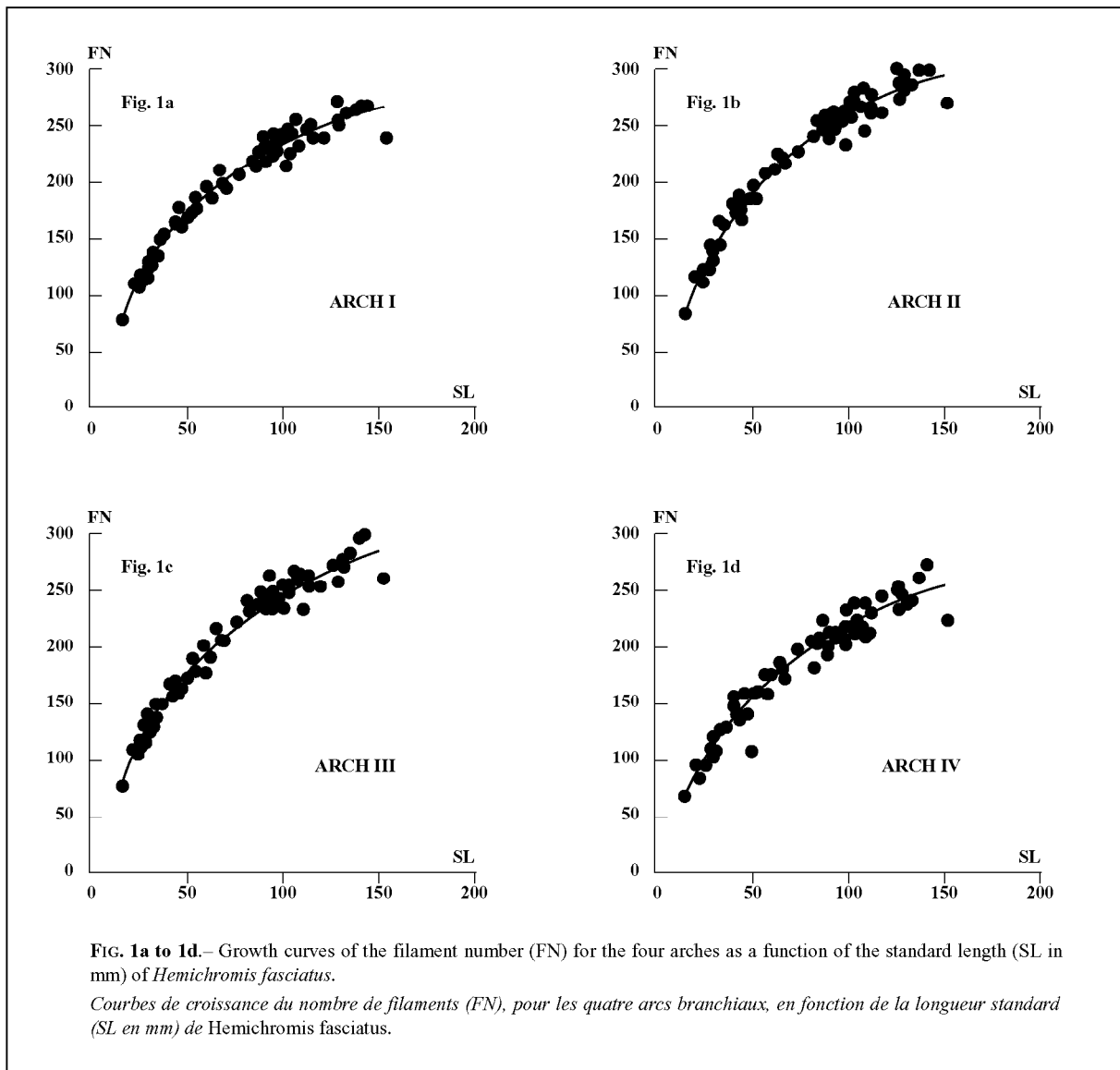


FIG. 1a to 1d.— Growth curves of the filament number (FN) for the four arches as a function of the standard length (SL in mm) of *Hemichromis fasciatus*.

Courbes de croissance du nombre de filaments (FN), pour les quatre arcs branchiaux, en fonction de la longueur standard (SL en mm) de Hemichromis fasciatus.

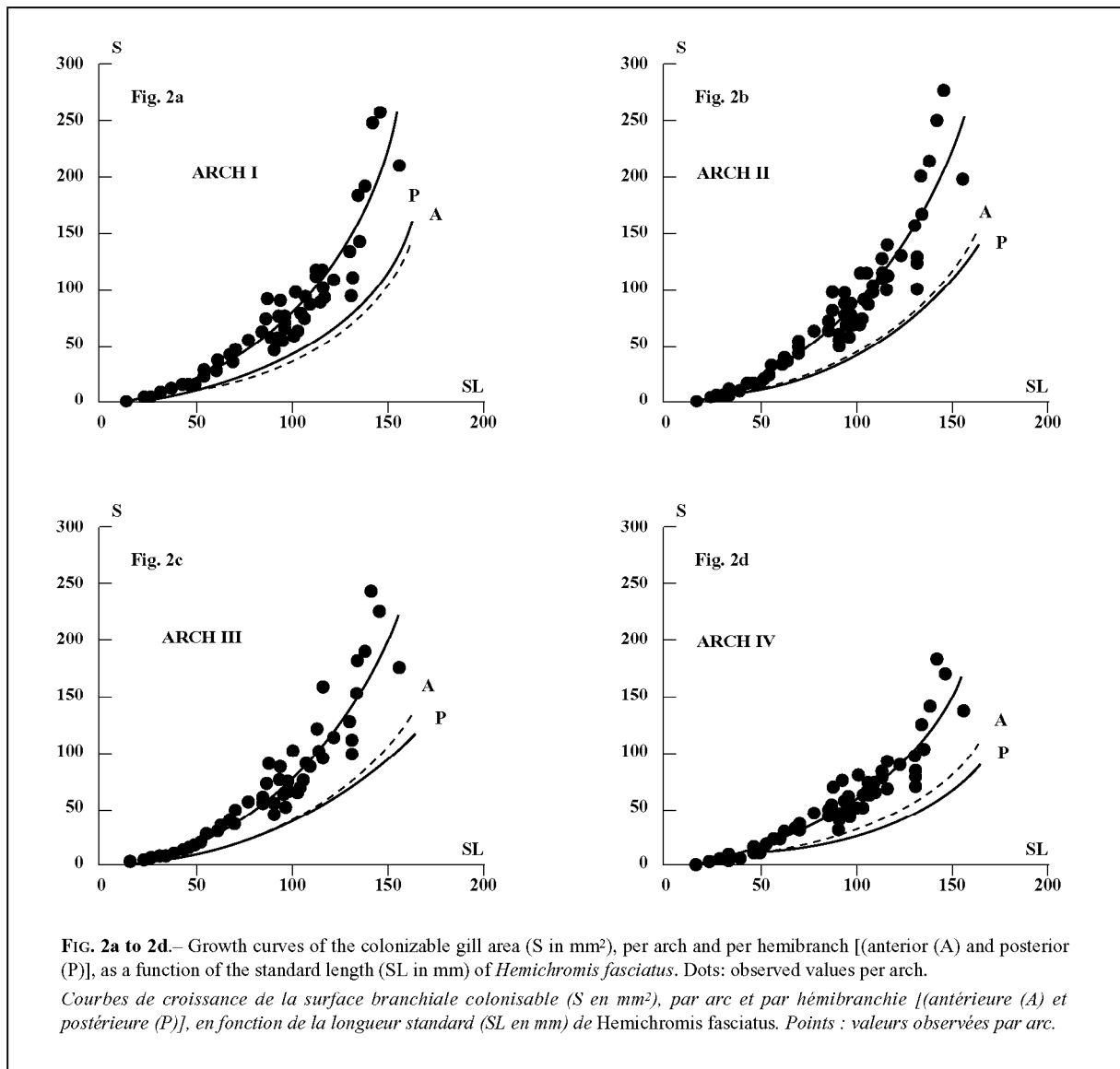
TABLE I.– Growth model equations of the filament number per arch.

Archs	Equations	S.E _r	S.E _s	S.E _b	S.E _c	S.E _k	S.E _l
Arch I	$F_N = 343,06 - 177,28e^{-0,03SL} - 165,78e^{-0,05SL}$	–	–	–	–	–	–
Arch II	$F_N = 322,37 - 266,43e^{-0,014SL} - 55,94e^{-0,05SL}$	$0,7 \cdot 10^{-2}$	$0,66 \cdot 10^{-1}$	100,739	128,092	0,008	0,070
Arch III	$F_N = 310,70 - 288,17e^{-0,014SL} - 22,53e^{-0,108SL}$	$0,2 \cdot 10^{-2}$	0,184	13,603	23,147	0,002	0,205
Arch IV	$F_N = 293,24 - 26-3,75e^{0,012SL} - 29,48e^{-0,083SL}$	$0,4 \cdot 10^{-2}$	0,130	17,668	37,851	0,004	0,142

y = F_N: filament number; x = SL: standard length;

S.E: standard error of equation parameters ($F_N = a + br^{SL} + cs^{SL}$ with $r = \exp(-k)$ and $s = \exp(-l)$);

missing values cannot be estimated using maximum likelihood and MLP



RESULTS

VARIATIONS IN GILL FILAMENT NUMBER

For the four successive and unilateral arches, figures 1a, 1b, 1c and 1d show the filament number variations in terms of the fish standard length. The best fitting function is of the type:

$$y = a + br^x + cs^x \text{ with } r = \exp(-k) \text{ and } s = \exp(-l)$$

For each gill arch, equation, parameters and standard errors associated are presented in Table I.

For all arches, the filament number increased rapidly at the beginning of the fish growth and tended to plateau. Its variability was slightly greater when the host length increased. Whatever the fish size, the filament number of arch IV variability was always lower than those of the other arches. Beyond a standard length of 30 millimeters, the filament number per arch decreased in the following order: II, III, I and IV.

VARIATIONS OF GILL AREAS

Figures 2a, 2b, 2c and 2d represent the colonizable area variation of each arch and its hemibranches [anterior (A) and posterior (P)] in terms of the fish standard length. The surface area growth can be fitted adequately by a polynomial function of degree 4. The related equations per arch and per hemibranch are presented in Table II.

For all arches, the colonizable gill area increased with the fish length. This growth intensified with increasing age. The arch IV area was distinctively lower than the oth-

ers. The colonizable surface area per arch decreased in the following order: II, I, III and IV. Except for arch I, the surface area of anterior hemibranches were generally greater than those of the corresponding posterior hemibranches.

COMPARATIVE APPROACH OF GILL GROWTH MODELS BETWEEN HEMICHROMIS FASCIATUS, DICENTRARCHUS LABRAX AND LIZA RAMADA

SILAN *et al.* (1987), then CALTRAN & SILAN (1996) have studied the gills of *Dicentrarchus labrax* and *Liza ramada* with the same modelling approach.

For the three host species, figure 3 shows the total number of filaments in the four successive and unilateral arches, in terms of the fish length. With the order of magnitude apart, growth models are similar. Although the lengths are different, the oldest *Hemichromis* have a filament number close to those of mature *Dicentrarchus* (> 300 mm). This number remains smaller for adult *Liza*. Though these data are not presented here, we can recall that the filament number per arch decreases in the following order: I, II, III and IV for *D. labrax*, and II, III, I, IV for *L. ramada*. Basing on this criterion, *H. fasciatus* is close to *L. ramada*. For the three host species, arch IV is always the smallest of the series.

For the three fishes, figure 4 displays the growth models of the total colonizable gill area in terms of the fish length. Once more, polynomial models are close. It is interesting to note that a 150-millimeter *Hemichromis* has a colonizable surface area equivalent to that of a 300-millimeter *Liza* or *Dicentrarchus*. It is quite logical between *Hemichromis* and *Dicentrarchus*, because of a similar

TABLE II.– Growth model equations of the colonizable surface area per arch and per hemibranch.

Archs	Equations	S.E a	S.E b	S.E c	S.E d	S.E e
Arch I	$S = -4,58SL + 0,30SL^2 - 3,14 \cdot 10^{-3} SL^4 + 1,32 \cdot 10^{-5} SL^4$	–	0,19	$6,98 \cdot 10^{-3}$	$0,17 \cdot 10^{-3}$	$0,1 \cdot 10^{-4}$
AH	$S = -1,84 \cdot 10^{-4} - 2,29 SL + 0,148SL^2 - 1,54 \cdot 10^{-3} SL^3 + 6,49 \cdot 10^{-6} SL^4$	0,09	$0,32 \cdot 10^{-3}$	$0,8 \cdot 10^{-4}$	–	–
pH	$S = 2,86 \cdot 10^{-4} - 2,29SL + 0,157SL^2 - 1,599 \cdot 10^{-3} SL^3 + 6,72 \cdot 10^{-6} SL^4$	0,106	$0,38 \cdot 10^{-2}$	$0,9 \cdot 10^{-4}$	–	–
Arch II	$S = -1,30SL + 0,15SL^2 - 1,03 \cdot 10^{-3} SL^3 + 4,99 \cdot 10^{-6} SL^4$	–	0,21	$7,63 \cdot 10^{-3}$	$0,19 \cdot 10^{-3}$	$0,1 \cdot 10^{-4}$
AH	$S = 3,32 \cdot 10^{-4} - 0,815SL + 8,31 \cdot 10^{-2} SL^2 - 6,087 \cdot 10^{-4} SL^3 + 2,92 \cdot 10^{-6} SL^4$	0,111	$0,39 \cdot 10^{-2}$	$0,10 \cdot 10^{-3}$	–	–
PH	$S = 1,29 \cdot 10^{-3} - 0,49SL + 6,84 \cdot 10^{-2} SL^2 - 4,165 \cdot 10^{-4} SL^3 + 2,06 \cdot 10^{-6} SL^4$	0,104	$0,37 \cdot 10^{-2}$	$0,9 \cdot 10^{-4}$	–	–
Arch III	$S = -0,33SL + 0,09SL^2 - 3,26 \cdot 10^{-4} SL^3 + 2,25 \cdot 10^{-6} SL^4$	–	0,20	$7,21 \cdot 10^{-3}$	$0,18 \cdot 10^{-3}$	$0,1 \cdot 10^{-4}$
AH	$S = -1,58 \cdot 10^{-3} - 0,54SL + 6,26 \cdot 10^{-2} SL^2 - 3,9 \cdot 10^{-4} SL^3 + 2,095 \cdot 10^{-6} SL^4$	0,102	$0,36 \cdot 10^{-2}$	$0,9 \cdot 10^{-4}$	–	–
PH-1	$S = 4,11 \cdot 10^{-3} + 0,21SL + 2,74 \cdot 10^{-2} SL^2 + 6,35 \cdot 10^{-5} SL^3 + 1,58 \cdot 10^{-7} SL^4$	0,102	$0,36 \cdot 10^{-2}$	$0,9 \cdot 10^{-4}$	–	–
Arch IV	$S = -2,34SL + 0,17SL^2 - 1,44 \cdot 10^{-3} SL^3 + 5,87 \cdot 10^{-6} SL^4$	–	$1,44 \cdot 10^{-3}$	$5 \cdot 10^{-3}$	$0,13 \cdot 10^{-3}$	–
AH	$S = -2,05 \cdot 10^{-3} - 1,325SL + 9,32 \cdot 10^{-2} SL^2 - 8,24 \cdot 10^{-4} SL^3 + 3,39 \cdot 10^{-6} SL^4$	0,079	$0,28 \cdot 10^{-2}$	$0,7 \cdot 10^{-4}$	–	–
PH	$S = 1,82 \cdot 10^{-3} - 1,012SL + 7,31 \cdot 10^{-2} SL^2 - 6,11 \cdot 10^{-4} SL^3 + 2,47 \cdot 10^{-6} SL^4$	0,067	$0,24 \cdot 10^{-2}$	$0,6 \cdot 10^{-4}$	–	–

S: colonizable surface area; SL: standard length; AH: anterior hemibranch; PH: posterior hemibranch
 S.E: standard error of equation parameters ($S = a + bSL + cSL^2 + dSL^3 + eSL^4$);
 missing values cannot be estimated using maximum likelihood and MLP

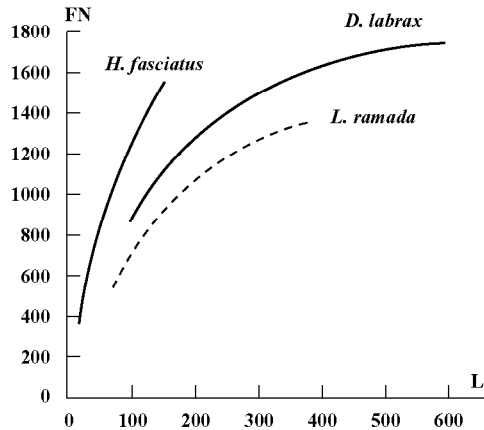


FIG. 3.— Growth curves, for three teleost species, of the total filament number (FN)(four unilateral arches) as a function of their length (in mm)(standard length (SL) for *Hemichromis fasciatus*; fork length (FL) for *Liza ramada* (adapted from CALTRAN & SILAN, 1996) and *Dicentrarchus labrax* (adapted from SILAN *et al.*, 1987).

*Courbes de croissance, pour trois espèces de téléostéens, du nombre total de filaments (FN) (quatre arcs unilatéraux) en fonction de leur longueur (en mm) (longueur standard (SL) pour *Hemichromis fasciatus*; longueur furcale (FL) pour *Liza ramada* (d'après CALTRAN & SILAN, 1996) et *Dicentrarchus labrax* (d'après SILAN *et al.*, 1987).*

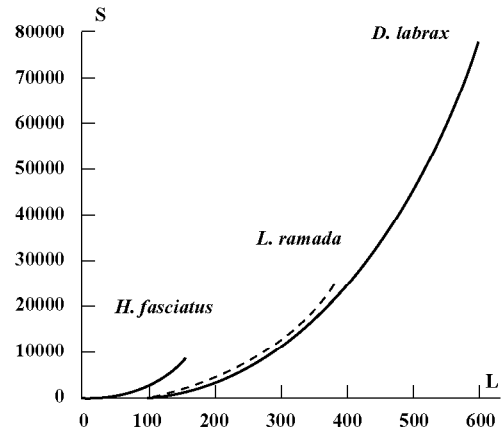


FIG. 4.— Growth curves, for three teleost species, of the total colonizable gill area (S in mm²) (four unilateral arches) as a function of their length (in mm)(standard length (SL) for *Hemichromis fasciatus*; fork length (FL) for *Liza ramada* (adapted from CALTRAN & SILAN, 1996) and *Dicentrarchus labrax* (adapted from SILAN *et al.*, 1987).

*Courbes de croissance, pour trois espèces de téléostéens, de la surface branchiale colonisable totale (S en mm²) (quatre arcs unilatéraux) en fonction de leur longueur (en mm) (longueur standard (SL) pour *Hemichromis fasciatus*; longueur furcale (FL) pour *Liza ramada* (d'après CALTRAN & SILAN, 1996) et *Dicentrarchus labrax* (d'après SILAN *et al.*, 1987).*

number of filaments for these lengths. On the other hand, *Liza* has a surface area comparable to that of *Dicentrarchus*, although its filament number is smaller than that of the sea bass for the same length. This is due to the heterogeneity of shape and length between filaments for *Liza*, and to a more pronounced increase of their depth with host age (CALTRAN & SILAN, 1996).

DISCUSSION & CONCLUSION

For *Hemichromis fasciatus*, as for some other teleosts (SILAN *et al.*, 1987; ROUBAL, 1987; CALTRAN & SILAN, 1996), the gill filament number increases with fish maturation but tends to stabilize. On the other hand, the gill area potentially colonized by ectoparasites is subject to a continuous growth without detectable limit. Results are similar for the four host species studied by the above authors regarding these points, whatever the method chosen for the estimation of the surface area.

The gill arches are not strictly equivalent in the same fish individual. The structure of these arches changes with host age in the same fish species. Whatever the species considered, the anterior arches are generally greater than the posterior. Only decreasing order between the three first arches is subject to variations, the fourth remaining smaller.

The fish gills are a potential biotope and a changing environment for numerous ectoparasites. They are subject to structure modifications having serious outcomes pointed out by SILAN *et al.* (1987), SILAN & LE POMMELET (1995), then CALTRAN *et al.* (1995a et b) in ectoparasite ecology. The gill filaments are elementary areas in which ectoparasites (Monogenea, Copepoda...) can directly settle, then their number and their distribution amongst arches are important. The local or total colonizable gill areas are not equivalent between fish species: slightly more than 100 cm² for the four arches of the largest *Hemichromis*, but 250 cm² for the largest *Liza* and about 800 cm² for the largest *Dicentrarchus* studied. These facts cannot be ignored when

studying spatial organisation of parasite communities. These differences are all the more important since host species do not have the same parasitic richness and specific diversity. For example *Hemichromis fasciatus* has eight species of monogeneans, *Liza ramada* six and *Dicentrarchus labrax* three. All these elements taken into account will cast new light on the study of relationships between available resources (food, space...), their variability, and structures of these parasite communities.

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VERSION FRANCAISE ABRÉGÉE

Les systèmes Hôtes-Parasites permettent diverses approches de l'étude des structures spatiales et de leurs variations dans ces communautés.

Tout organe d'un hôte, s'il est colonisé par plusieurs espèces parasites, constitue un biotope pour cette communauté. À l'échelle de l'individu-hôte, ce biotope est qualifié "d'élémentaire" (SILAN *et al.*, 1987). La reproductibilité de ces unités élémentaires permet l'analyse comparative de communautés homologues, ou de guildes homologues si les espèces concernées sont taxinomiquement et écologiquement proches. Une connaissance précise de ces biotopes est donc nécessaire dans le cadre d'une approche fonctionnelle.

L'hétérogénéité du biotope branchial des poissons a été soulignée (SILAN *et al.*, 1987; ROUBAL 1987; SILAN & LE POMMELET, 1995; CALTRAN & SILAN, 1996). Cette hétérogénéité est associée à la structure des branchies de l'hôte (nombre et forme des filaments branchiaux, surface branchiale colonisable), laquelle varie dans l'espace et dans le temps. Dans l'espace, car un tel organe n'est pas homogène à l'échelle de l'individu-hôte. Dans le temps, parce que des modifications de diverses natures interviennent au cours de la croissance des hôtes; le nombre de filaments et leur surface colonisable par les parasites augmentent, par exemple, avec l'âge du poisson, sans que les relations de densité ou d'intensité-dépendance qui en découlent soient simples.

Les contraintes environnementales que subissent les parasites (facteurs environnementaux externes, hydrodynamisme...), ainsi que la quantité de ressources disponibles, vont ainsi dépendre de cette variabilité de structure.

Hemichromis fasciatus Peters, 1858, un Cichlidae africain (Teleostei), est parasité par huit espèces d'Ancyrocephalidae (Monogenea) (BILONG BILONG & EUZET, 1995). Ces ectoparasites coexistent sur ses branchies et se partagent les différentes ressources (espace, nourriture...) de ce biotope. Les changements dans la structure des branchies ont été étudiés au cours de la maturation de l'hôte. L'augmentation du nombre de filaments peut ainsi être décrit par un modèle exponentiel, et la croissance de la surface branchiale colonisable par une fonction polynomiale. Ces modèles sont comparés avec ceux de deux téléostéens des milieux tempérés : *Dicentrarchus labrax* (LINNÉ, 1758) (Moronidae), étudié par SILAN *et al.* (1987), et *Liza ramada* (RISSO, 1826) (Mugilidae), analysé par Caltran & Silan (1996). Les conséquences écologiques des diverses variations de structure sont introduites.