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Hervé Caltran, Patrick Silan. The ectoparasite community of *Liza ramada*: population interactions and variable environments. 2012. hal-00761059

HAL Id: hal-00761059

<https://hal.science/hal-00761059>

Submitted on 5 Dec 2012

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The ectoparasite community of *Liza ramada* : population interactions and variable environments

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ABSTRACT

In the Vaccares lagoon (Rhône delta, Camargue, France), mullets of the species *Liza ramada* (Pisces, Teleostei) are parasitized by seven metazoan species, ectoparasites of gills : six Monogenea and one Copepoda. The spatial and temporal structures of this parasite community were analysed. The host migrates within this delta in the course of the seasons, and its parasites are potentially affected by the fluctuating environmental constraints. The crossed effects between the structure of the parasite infrapopulations and some environmental characteristics were studied with a co-inertia analysis. This study emphasizes the interactions between the populations structures and the environment, and their consequences on local biodiversity.

KEY WORDS

Lagoon ecosystem ; *Liza ramada* ; Fish ; Host-parasite relationships ; Population biology ; Community ecology : Co-inertia analysis.

INTRODUCTION

Ecology of parasitic populations or communities is the object of an increasing attention since two or three decades. Among the studied questions, the organisation of communities has been explored ; nevertheless studies about marine ectoparasite communities in natural and unstable aquatic ecosystems are not so frequent (Silan *et al.*, 2003).

Parasite populations are fragmented and display most often high spatial and temporal heterogeneities, dependent on complex demographic processes (Silan *et al.*, 1997). Identification of local patterns and analysis of interactions at the infrapopulation level are then more informative (Silan and Maillard, 1990 ; Bouloux *et al.*, 1998).

The gill ectoparasite xenocommunity (Combes, 1995) of the mullet *Liza ramada* (Risso 1826), the relationships among the different species and environmental constraints, are studied here with a multiway data analysis. Host and parasite populations are partly isolated in a deltaic ecosystem, and both are potentially affected by environmental constraints that change in space and time.

METHODS

1) Environment and species

The site (Rhône delta, Camargue, France) and sampling techniques of hosts and parasites have been already described in previous works (Caltran *et al.*, 1995a, 1995b). The present study concerns 241 *Liza ramada* ; thirty three of these hosts were parasite free.

Three environmental variables were taken account : the three host sampling sites (Fumemorte canal, mouth of this canal in the Vaccares lagoon, and the lagoon itself (Romieu)), four seasons (Winter = W, Spring = Sp, Summer = Su, Fall = F) and six host ages (0+, 1+, 2+, 3+, 4+, 5+) according to the growth model determined by Autem (1979). Notations 0+ indicate that individuals are in their first year, 1+ the individuals which are one year old and so on. The environmental table is composed of 241 rows (host individuals) and 13 columns (above mentioned modalities). The modalities are disjunctive.

The gill parasite community of *Liza ramada* studied here is composed of :

- Five species of Monopistocotylea (Monogenea) with four Ancyrocephalidea (*Ligophorus imitans*, *L. confusus*, *L. parvicirrus*, *Ergenstrema mugilis*) (Euzet and Suriano, 1977 ; Lambert and Sanfilippo, 1977 ; Euzet and Sanfilippo, 1983) and one Gyrodactylidea (*Gyrodactylus sp.*) ;
- One species of Polyopistocotylea (Monogenea) : *Microcotyle mugilis* (Euzet and Combes, 1969) ;
- One Copepod (Crustacea) : *Ergasilus lizae* (Raibaut and Ben Hassine, 1977 ; Ben Hassine and Raibaut, 1980).

All these species colonize the gill filaments except *E. mugilis* which live on the gill rakers. 8449 parasites (database) are concerned by this analysis.

When the stage of maturity can be established for a given species, it can indirectly inform about the age of the parasite (Silan and Maillard, 1989a), and can thus be a useful demographic descriptor for a population analysis (Bouloux *et al.*, 1998). Three of these stages (juvenile, young and old adults) can be defined for *L. imitans*, and then have been used.

The table of species (faunistic table) was composed of 241 rows (host individuals) and 9 columns (7 parasites species, one of which (*L. imitans*) described by the three maturity stages above mentioned). All values of the faunistic table (varying from 0 to 1050) was log transformed ($\log (X_i+1)$).

2) Mathematical method

We used a co-inertia analysis (Chessel & Mercier, 1993 ; Dolédec & Chessel, 1994), a numerical approach based on the euclidian model for a symmetrical study of species-environment relationships. Two standard multivariate analyses allow in a first step to isolate inertia axes ; the first analysis (correspondence analysis – CA) concerns the faunistic table, and the second (multiple correspondence analysis – MCA) the environmental table. Then both analyses are coupled, the mathematical problem being to maximize the covariance of the projected scores which result from the two first analyses. New co-inertia axes are isolated (Fauna and environmental axes). The statistical significance of eigenvalues or inertia may be

tested using Monte Carlo permutation tests (Fraile *et al.*, 1993). The analysis, calculations and graphs were performed using the software A.D.E. (Thioulouse *et al.* 1997).

Prevalences (P) and mean intensities (MI) associated with some samples were calculated.

RESULTS

The 33 *L. ramada* without parasite (table I) are essentially young fishes (0+, 1+) caught in spring or summer. Nevertheless, hosts free of parasite can be observed whatever the sites, seasons or host ages.

Sampling sites	Seasons	Age	Fish numbers
Fumemorte	Winter	2+	1
	Spring	2+	2
		4+	2
	Fall	1+	1
		5+	1
Mouth of canal	Winter	0+	1
		1+	1
		3+	2
	Spring	0+	1
		2+	1
	Summer	0+	7
		1+	9
		1+	2
	Fall	2+	1
1+		1	
Romieu	Winter	1+	1
Total			33

Table I

The results of the preliminary analyses (CA and MCA) help only for the interpretation, and their details are consequently not developed here.

The graph of eigenvalues (Fig. 1a) indicates that the two first axes are preponderant and represent 72,8 % of the inertia. The F1/F2 co-inertia plan corresponds almost to the F3/F1 plan of the CA (fauna data)(Fig. 1b), and to the F1/F2 plan of the MCA (environmental data)(Fig. 1c).

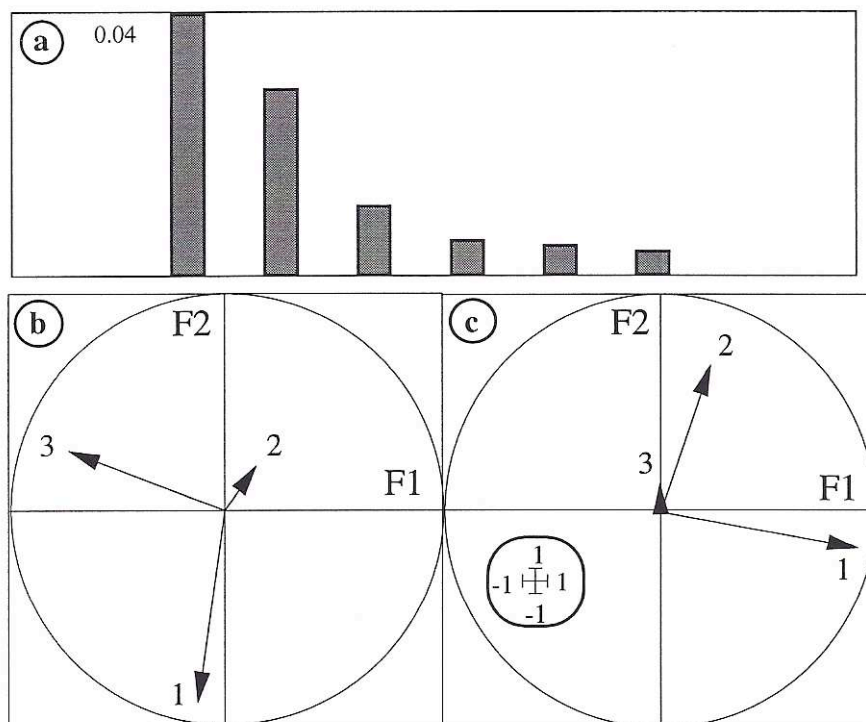


Fig. 1 : Co-inertia analysis – 1a : Graph of eigenvalues ; 1b et 1c : Projection of the three first inertia axes of the separate analyses in the F1/F2 co-inertia plan ; 1b : correspondence analysis (CA) with the faunistic table ; 1c : multiple correspondence analysis (MCA) with the environmental table.

The comparison of the inertia resulting from the co-inertia analysis with that resulting from the distinct analyses of each data set (CA on faunistic table and MCA on environmental table) is presented in the table II.

AXIS	InerF	InerE	VarF	VarE	Covar	Correlation
F1	0,35	0,60	0,23	0,55	0,21	0,59
F2	0,33	0,48	0,30	0,36	0,17	0,51

Table II

With : InerF and inerE : maximal projected inertia of the faunistic (InerF) and environmental (InerE) tables ; VarF and VarE : inertia of the the faunistic (VarF) and environmental (VarE) tables projected on the co-inertia axes ; Covar : Covariance of the two sets of coordinates projected on the co-inertia axes ; Correlation : correlation between the two new sets of coordinates resulting from the co-inertia analysis.

For F1, InerF (0,35) is slightly higher than VarF (0,23) ; the same observation can be made between InerE (0,60) and VarE (0,55). For F2, the situation is similar. The observed correlations (0,59 and 0,51) are enough high to consider that a co-structure exists.

Fig. 2 shows the frequency distribution of the co-inertia calculated after 500 random simulations. The observed inertia is always greater than values calculated after permutations.

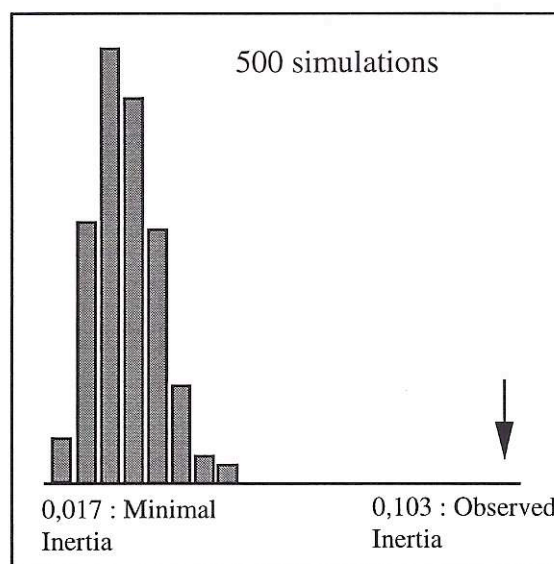


Fig. 2 : Frequency distribution of the co-inertia calculated after 500 random permutations and co-inertia observed

Figs 3a1, 3a2 and 3a3 show the projections of the 3 environmental variables and of their 13 modalities in the F1/F2 co-inertia plan.

These plans underline the structure of these host samples : i) the most important gradient concerns the age of the hosts (Fig. 3a3) ; ii) the youngest fishes come principally from the Vaccares lagoon (Fig. 3a1), and have been caught during the coldest seasons (Fig. 3a2) ; iii) the oldest mullets have been captured during the fall, some in summer (Fig. 3a2), and essentially in freshwater (Fumemorte)(Fig. 3a1). The sampling structure can be explained with the biology of these different cohorts of mullets in this ecosystem (Caltran *et al.*, 1995a). The axis F2 isolates mullets of the mouth sampled during the fall from those sampled in winter.

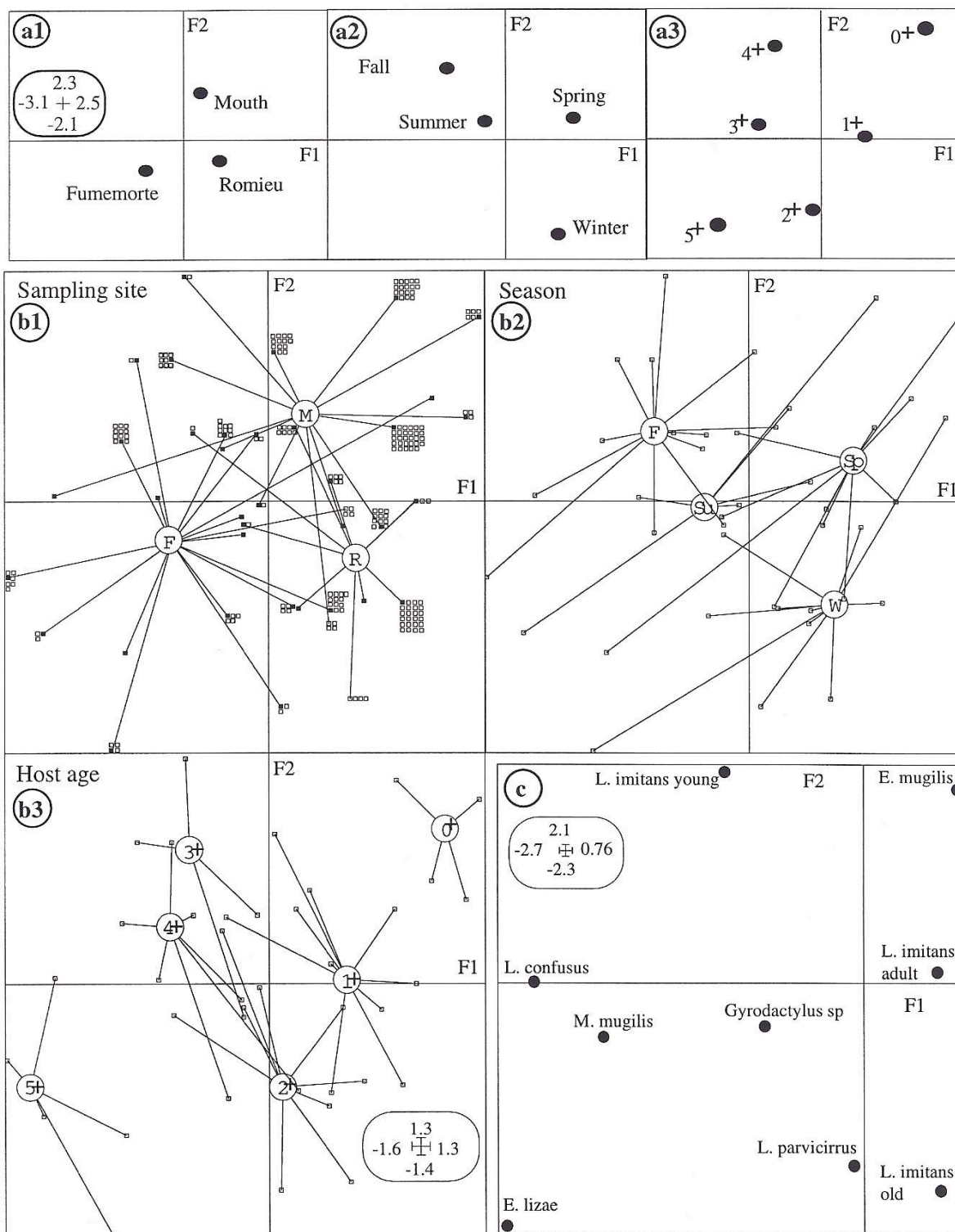


Fig. 3 : 3a : Projections of the 3 environmental variables and their modalities in the F1/F2 co-inertia plan (3a1 : sampling sites ; 3a2 : season ; 3a3 : host age). 3b : Projections of the host individuals (squares) in the F1/F2 co-inertia plan (3b1 : sampling sites ; 3b2 : season ; 3b3 : Host age ; white squares of 3b1 = superposed points). 3c : Projections of the parasite species or their maturity stages in the F1/F2 co-inertia plan.

Fig. 3b1 represents all host individuals in the F1/F2 co-inertia plan, located according to their coordinates resulting from the analysis about the environmental table, and for the variable « site of sampling ». Each individual, represented by a square (the white squares near black squares represent superposed host individuals), is linked to the modality at which it belongs to (center of gravity). Figs 3b2 and 3b3 are established according to the same principles, but for the two other variables (3b2 for the « season » and 3b3 for the « age of the host »). The fishes being the same that in Fig. 3b1, superposed points are not represented in Figs. 3b2 and 3b3. The figures 3b1, 3b2 and 3b3 illustrate the observed tendencies of Figs 3a1, 3a2 and 3a3, but especially detail the structure and the diversity of the host samples.

Fig. 3c shows the projections of parasite species or their stages of maturity (*L. imitans*) in the F1/F2 co-inertia plan. The axis F1 separates *L. confusus*, *E. lizae*, *M. mugilis* (negative coordinates) and *E. mugilis*, *L. imitans* - adult or young (positive coordinates). The axis F2 distinguishes in particular the stages of maturity of *L. imitans*, as well as *L. parvicirrus* from *E. mugilis*.

The position of the species in F1 is partly linked to their respective abundance, but also to their relationships with the environmental variables. The most frequent species or stages are centred : adult *L. imitans* (P = 79,25%, MI = 22,15), *Gyrodactylus sp.* (P=33,19%, MI = 21,35). Old *L. imitans* (P = 24,48%, MI = 9,81), *E. mugilis* (P = 23,24%, MI = 3,18), and especially *E. Lizae* (P = 5,39%, MI = 1,77) or *L. parvicirrus* (P = 4,98%, MI = 1,67) are the most irregular or rarest. Young *L. imitans* (P = 19,92%, MI = 3,73) and *M. mugilis* (P = 4,56%, MI = 1,36) have a particular status underlined by the axis F3 (not represented here), due to a combination *M. mugilis* / young *L. imitans* / old *L. imitans* absent, without strong ecological meaning.

Taking all ages together, *L. imitans* is the dominant species and is alone in 28% of the cases. In 28 associations made up of 2 to 5 species, it is present 25 times.

L. confusus, *L. parvicirrus*, *E. mugilis*, *Gyrodactylus sp.* and *E. lizae* were found alone, but in less than 0,4% of the cases. *M. mugilis* was never found alone. The most frequent associations are *L. imitans* / *L. confusus* (10,4%) and *L. imitans* / *Gyrodactylus sp.* (10%).

The relative positions of the species and maturity stages in the factorial plans depend on frequencies of associations between them, and on the number of parasites concerned in these associations.

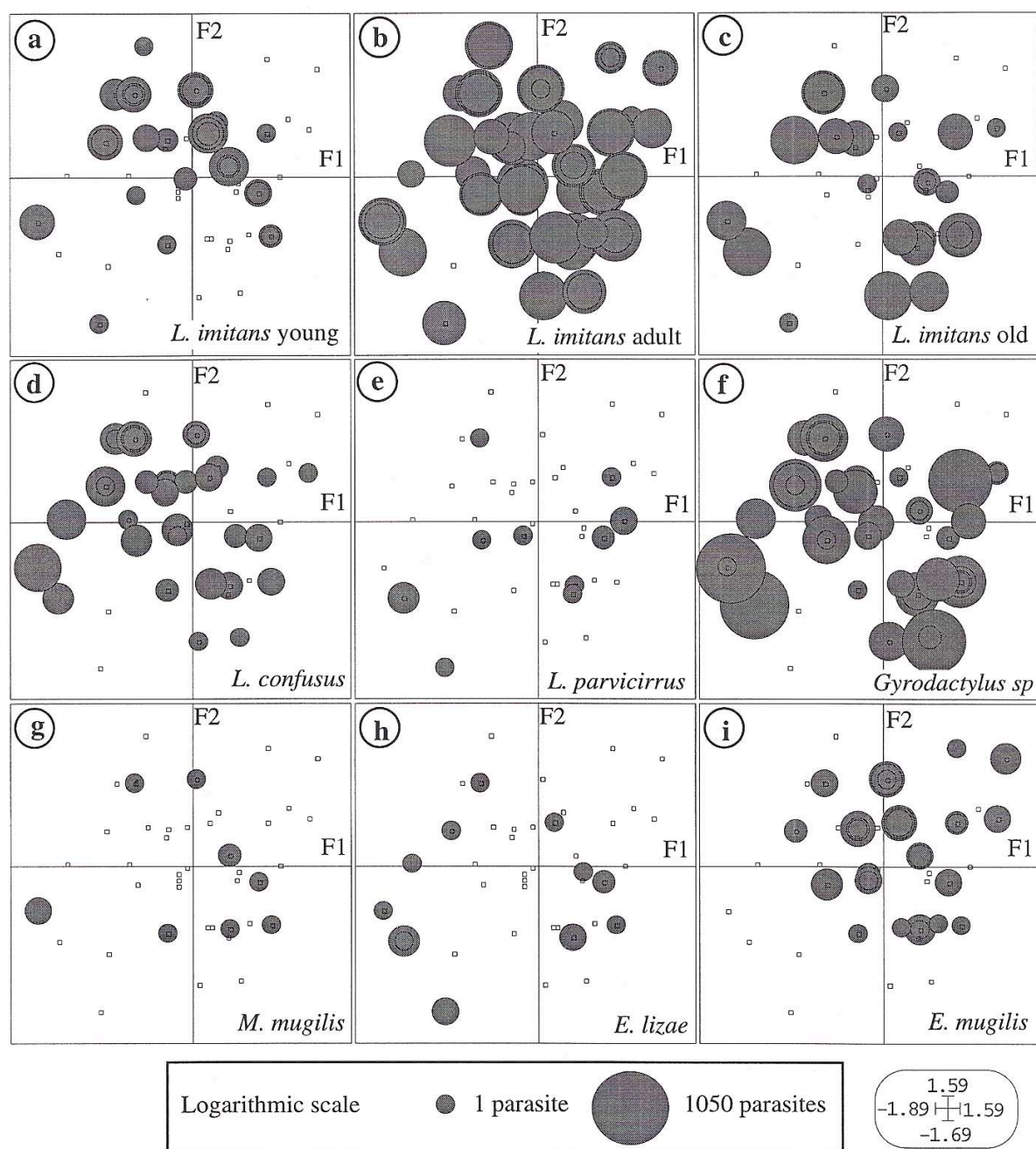


Fig. 4 : Projections of the host individuals (squares) in the F1/F2 co-inertia plan, using the co-inertia weights of the corresponding faunistic variables (4a : *L.imitans* young ; 4b : *L. imitans* adult ; 4c : *L. imitans* old ; 4d : *L. confusus* ; 4e : *L. parvicirrus* ; 4f : *Gyrodactylus* sp. ; 4g : *M. mugilis* ; 4h : *E. lizae* ; 4i : *E. mugilis*).

Figs 4a to 4i give new details and illustrate this last fact. They show the distribution of species (or stages for *L. imitans*) in the double space « host individuals / environment », and then the relationships between the host individuals and each variable of the faunistic table. The grey circles represent the parasitised fishes. The size of each circle is dependent on the number of parasites (Intensity) on the corresponding fish. The small squares represent the mullets without specimen of the considered species.

Young *L. imitans* (Fig. 4a) are present on fishes of different ages except on the individuals of age 0+ (cf. Fig. 3b3). That does not necessarily mean that these fishes cannot be parasitized with *L. imitans* since the adults are present (Fig. 4b), but this cohort could be less easy to parasitize. The recruitment of larvae is effective all year long, because young *L. imitans* can be observed in any season. Intensities are the highest during the warmest periods (Summer, Fall), and the number of fish parasitised with young *L. imitans* is also more important during these seasons (cf. Fig. 3b2). These elements mainly explain the coordinates of this variable in Fig. 3c.

The central position of adult *L. imitans* in Fig. 3c becomes clearer when its demographical status is established as in Fig. 4b. They colonize enough intensively all cohorts of mullets during any seasons.

The old *L. imitans* (Fig. 4c) are present also on all mullets, but they are a little more rare on the youngest fishes (cf. Fig. 3b3). A very slight increase of their presence or of their intensities is noted during the coldest seasons, in particular in winter (cf. Fig. 3b2). That explain partly the coordinates of this variable in Fig. 3c.

L. confusus (Fig. 4c) is observed on *L. ramada* of different ages, but is rarer on the youngest mullets (cf. Fig. 3b3). This species is present any season, but its intensities slightly increase during the fall (cf. Fig. 3b2), and on fishes older than 3 years (cf. Fig. 3b3).

In this environment, *L. parvicirrus* (Fig. 4e) is a scarce species, but is present all year long (cf. 3b2). It has never been found on the youngest mullets (cf. Fig. 3b3), and has principally been observed in winter and on 1 or 2 years old fishes. That explain the coordinates of this variable in Fig. 3c.

Gyrodactylus sp. (Fig. 4f) is a omnipresent species and its status is similar to that of *L. imitans*. It is observed all year long and on all kinds of host individuals.

M. mugilis (Fig. 4g) is a rare species, observed in any season, but absent on the youngest mullets (cf. Fig. 3b2). That explain the coordinates of this species on the axis F1 in Fig. 3c.

E. lizae (Fig. 4h) is not very frequent, but is observed all year, in all sites studied, on any type of fishes except on the youngest ones. Its presence on the oldest hosts caught in fresh water (cf. Fig. 3b1) explains its off-centered position in Fig. 3c.

E. mugilis (Fig. 4i) is absent from the oldest hosts (cf. Fig. 3b3), but is enough frequent on the immature fishes. That explain the coordinates of this species in the plan F1/F2 of Fig. 3c.

DISCUSSION AND CONCLUSION

L. imitans is the most numerous and widespread species, living in the fresh water and saltwater. It is the central species of the xenocommunity, reproduces during all seasons ; however its reproduction is certainly facilitated when the temperatures are not extreme, as it's the case for the others Monopisthocotylea (Silan and Maillard, 1989a). For *Ancyrocephalus vanbenedenii*, ectoparasite of *Mugil cephalus*, Mac Rawson (1976) described a decrease of the prevalences and intensities in summer and in the fall. Euzet and Suriano (1977), Euzet and Sanfilippo (1983) showed since that *A. vanbenedenii* was in fact a complex of several distinct congeneric species (Euzet and Combes, 1980), including *L. imitans* which has a specific demographic behavior.

L. confusus has a demographic strategy similar to that of *L. imitans*, but is generally less abundant. *L. confusus* is more easily present on the older fishes.

The population structures of *L. imitans* and *L. confusus* have common traits with the ones described for both *Diplectanum* of the sea bass (Silan and Maillard, 1989a, 1990).

L. parvicirrus is present all year long but remains rare. The observed increase of some infrapopulations in winter cannot be ecologically interpreted.

In 1983, Euzet and Sanfilippo have studied 78 *L. ramada* of the same lagoon and have observed the following prevalences : 81% for *L. imitans* , 0% for *L. confusus* and 36% for *L. parvicirrus*. In this analysis, they are respectively equal to 80.9%, 27.38% and 4.98%. The environment of this lagoon is subject to change in the course of decades (Aguesse & Marazanoff, 1965 ; Heurtaux, 1992), in particular of salinity, with an obvious impact on the structure of these populations (Silan *et al.*, 2003).

Gyrodactylus sp. is common and even very abundant on some host individuals. From a biological point of view, this monogenean is very different from the 3 Ancyrocephalidea (*Ligophorus*). *Gyrodactylus sp.* does not lay eggs, its larvae do not swim but parasitize fishes by contact (Bakke *et al.* 1992). Consequently an infrapopulation is able to grow directly on a same host individual. Furthermore, the reproduction of these worms is known to be largely dependent on the temperature in fresh water (Gelnar, 1987). The control of the parasitic populations by the host has already been noted for some Gyrodactyloidea, reducing in this way the new infestations (Lester and Adams, 1974 ; Scot and Anderson, 1984). If there is such a control for *L. ramada*, it is in all likelihood for very large intensities, because some of them are parasitized by more than 1000 *Gyrodactylus*.

M. mugilis is never common, as a lot of Polyopisthocotylea (Silan and Maillard, 1989b ; Reversat *et al.*, 1992). These monogeneans have difficulties to colonize the youngest hosts, their intraspecific competition is effective, and their presence or their abundance are dependent on ecology or on the behaviors of the host individuals.

The copepod *E. lizae* has low intensities (< 6), what is usual for these "large-sized" organisms. This species can live in fresh water (Kelly and Allison, 1962), and its biological cycle take place normally in this kind of environment (Braun, 1981).

E. mugilis is the only species of this parasitic community living on the gill rakers. Like *L. imitans*, it easily parasitizes the youngest fishes, whatever the place. *E. mugilis* is on the other hand uncommon on the oldest mullets. These ectoparasites have small hooks, and the

hydrodynamical constraints could be for them a limiting factor in the greatest gill biotopes (Silan and Le Pommelet, 1995 ; Caltran and Silan, 1996 ; Bilong Bilong *et al.*, 1999).

The structure of this ectoparasite community present the following general characteristics :

- The dynamics of these populations do not display a marked periodicity, like often observed for the Monogeneans of inland waters. The variations of abiotic factors have a limited influence for these species during the year. The local and temporary migrations of some mullets do not radically change the population structures, even if some demographic parameters (fecundity, survival rate...) are very likely modified (Silan & Maillard, 1989a).

- Such populations are very heterogeneous units, and we see the interest to study them in a multidimensional context. The demography of these populations, as well as the structure of such community, are the result of a combination between determinist and stochastic processes (Langlais and Silan, 1995 ; Silan *et al.*, 1997 ; Bouloux *et al.*, 1998 ; Silan *et al.*, 1999 ; Silan *et al.*, 2003).

- The comparison of these results with other data (Euzet and Sanfilippo, 1983) show that long-term environmental changes can lead to a modification of the dominance relationships between the species, even to a substitution. This fact can have fundamental consequences from a biogeographic or evolutive viewpoint (Silan *et al.*, 2003).

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