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COMPARATIVE POPULATION BIOLOGY OF FISH DIGENES: THE CASE OF THREE *HELICOMETRA* (TREMATODA: OPECOELIDAE) MESOPARASITES OF MARINE TELEOSTS IN A MEDITERRANEAN LAGOON

J. REVERSAT, P. SILAN*

SUMMARY

In the Etang de Thau (Hérault, France), three species of *Helicometra* parasitize in their adult stage the digestive tract of the black goby *Gobius niger*, the grass goby *Zosterisessor ophiocephalus*, the grey wrasse *Symphodus cinereus*, and the common eel *Anguilla anguilla* (Teleostei). These fish act as definitive hosts in the biological cycle of these plathyhelminths. Also *H. gobii* exists in *G. niger*, *Z. ophiocephalus*, *S. cinereus* and *A. anguilla*; *H. fasciata* is found in *G. niger*; and *H. pulchella* is only found in *S. cinereus*. In the case of the two gobies and the eel, these three congeneric digenes sometimes coexist in the same infracommunity. Spatio-temporal analysis of these different populations has enabled: 1) detection of seasonal variations in their structure,

2) identification of the relationships between the nature of their specificity and demographic strategy, and 3) the global absence of statistical dependence between the intensities of different species in the same infracommunity to be shown. Implications arising from previous research concerning the demographic behaviour of these trematodes in their first intermediate host (mollusc compartment), were taken into account when interpreting structures observed in the definitive hosts. The problems of coexistence between these species, which are taxonomically very close in the same parasite community, and the under-lying speciation mechanisms are discussed in the light of population structuration.

RÉSUMÉ : Biologie comparée des populations de Digènes de Poissons : le cas de trois *Helicometra* (Trematoda: Opecoelidae) mésoparasites de Téléostéens marins dans un étang méditerranéen.

Dans l'Étang de Thau (Hérault, France), trois espèces d'*Helicometra* parasitent à l'état adulte le tube digestif du gobie noir, du gobie jaune, de la clavière et de l'anguille (Téléostéens). Ces poissons représentent l'hôte définitif dans le cycle biologique de ces plathelminthes. Ainsi, *H. gobii* est présent chez *Gobius niger*, *Zosterisessor ophiocephalus*, *Symphodus cinereus*, et *Anguilla anguilla*; *H. fasciata* se rencontre chez *G. niger*, *Z. ophiocephalus* et *A. anguilla*; *H. pulchella* ne parasite que *S. cinereus*. Chez les deux gobies et l'anguille, ces trois espèces congénériques coexistent parfois dans le même infrapeuplement. L'analyse spatio-temporelle de ces différentes populations a conduit à détecter des variations saisonnières dans leur structuration, à identifier des

relations entre la nature de leur spécificité et leur stratégie démographique, et à montrer l'absence globale de dépendance statistique entre les effectifs de ces différentes espèces dans les mêmes infrapeuplements. Les implications du comportement démographique de ces trématodes chez leur premier hôte intermédiaire (compartiment mollusque), étudié dans un travail antérieur, ont été prises en compte pour interpréter les structures observées chez les hôtes définitifs. Enfin, les problèmes de la coexistence de ces espèces taxinomiquement très proches dans un même peuplement parasitaire, et des mécanismes sous-jacents de spéciation, sont discutés à la lumière de la structuration de ces populations.

INTRODUCTION

Few parasitologists have studied intestinal helminth communities in order to identify the nature of interactions between parasites in a host population (Schad, 1963; Holmes, 1973; Holmes and Price, 1986; Stock and Holmes, 1987; Holmes, 1990; Kennedy, 1990). Even though the amount of research has increased over the last twenty years, very little deals with the coexistence of congeneric species in

the same host population (Uglen and Beck, 1972; Kennedy and Moriarty, 1987).

In this work we propose to study certain characteristics of demographic strategies concerning three species of *Helicometra* Odhner, 1902 (Trematoda), which inhabit in their adult stage the digestive tract of marine teleosts. These have been genetically identified (Reversat *et al.*, 1989), and named respectively (Reversat *et al.*, 1991a) i) *H. gobii* which is present in black goby *Gobius niger*, grass goby *Zosterisessor ophiocephalus*, grey wrasse *Symphodus cinereus*, and eel *Anguilla anguilla*; ii) *H. fasciata* in *G. niger*, *Z. ophiocephalus* and *A. anguilla*; iii) *H. pulchella* which is only present in *S. cinereus*. We will also be analyzing the distribution of these three intestinal digenes in different host

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populations sampled, and discussing these results in the context of allocation of « host population » resource from both the spatial (Holmes, 1973; Bush and Holmes, 1986) and temporal (MacKenzie and Gibson, 1970) point of view. The problem concerning interaction between congeneric species will also be discussed.

The structure of these different parasite populations in their mollusc compartment having been analyzed elsewhere (Reversat and Silan, 1991), we will comment on the functional aspects associated with these populations in the light of results obtained from both the definite host, as well as the first intermediate host (Mollusc).

MATERIAL AND METHODS

Samples of adult fish [*G. niger* (Gobiidae), *Z. ophiocephalus* (Gobiidae), *S. cinereus* (Labridae) and *A. anguilla* (Anguillidae)] were collected in a Mediterranean lagoon, the Etang de Thau (France), all samples being taken between October (OR) 1987 and June (JE) 1988. Fish were examined and their *Helicometra* genetically analyzed in the manner described previously by Reversat *et al.* (1989). Data from 214 *G. niger*, 432 *S. cinereus*, 230 *A. anguilla* and 498 *Z. ophiocephalus* from the Etang de Thau were available. Figure 1 shows the monthly catches of these four teleosts.

The absence of samples during the months of July, August, and September, together with their scarcity in June are due to almost non-existent fishing of these hosts during the hot part of the year. Statistical comparisons between independent samples with non-homogeneous variances were carried out using the Kruskal-Wallis H-test. When the comparisons relate to abundances, only positive values of this parameter are taken into consideration. Analysis of non-linear correlations was performed with Spearman's coefficient of rank correlation (R_s). In this last test, the null hypothesis was $H_0: R_s = 0$, and the alternative hypothesis $H_a: R_s > 0$ or $R_s < 0$. In the first case ($H_a: R_s > 0$), H_0 is rejected if $Z_{R_s} \geq Z_\alpha$ with $n > 30$ and if $R_s \geq R_{st}$ with $n \leq 30$; in the second case ($H_a: R_s < 0$), the hypothesis H_0 is rejected if $Z_{R_s} \leq -Z_\alpha$ with $n > 30$ and $R_s \leq -R_{st}$ with $n \leq 30$ (Scherrer, 1984).

Prevalence (P), mean intensity (MI) and abundance (A) are used

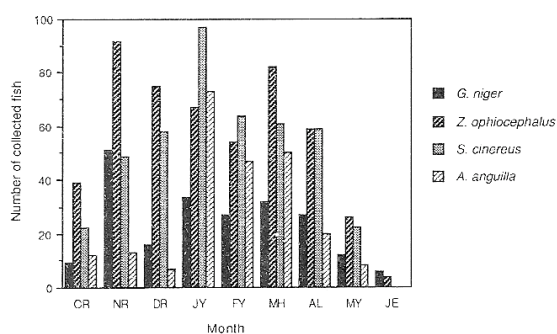


FIG. 1. — Number of teleosts (*G. niger*, *Z. ophiocephalus*, *S. cinereus*, *A. anguilla*) monthly collected.

OR : October, NR : November, DR : December, JY : January, FY : February, MH : March, AL : April, MY : May, JE : June.

as defined by Margolis *et al.* (1982). The term « global prevalence » will be used to describe the value of this parameter as applied to all the host samples used throughout the study.

RESULTS

1. TEMPORAL VARIATION OF PARASITISM

When studying temporal variations of these three *Helicometra* populations, the three following parameters were used: prevalence, mean intensity, and abundance.

1.1. *Helicometra gobii*

This digene exists in four of the teleost hosts under study (*G. niger*, *Z. ophiocephalus*, *S. cinereus* et *A. anguilla*). We see in Figure 2a that in the first two months of research (October and November), *H. gobii* was not present in any of the hosts.

a) In the case of *Gobius niger*, *H. gobii* is thus absent in autumn (nil prevalence in October and November) (Fig. 2a). Prevalence increases from the beginning of December, and reaches its peak in February ($P_{FY} = 59.3\%$). Of the four species of hosts parasitized by *H. gobii*, *G. niger* is the fish which is by far the most often infested; global prevalence reaches 30% over the whole of the study period. The Kruskal-Wallis test applied to abundances shows that no monthly value is statistically different from the others (H_0 not rejected with $H = 7.34$, $P > 0.05$, $DF = 6$) (Table I). Despite a slight increase in January ($MI_{JY} = 6.7$), mean intensities of different months (Fig. 2b) are not statistically different (H_0 not rejected with $H = 12.68$, $P > 0.05$, $DF = 6$). It is thus evident that the proportion of black gobies infested by *H. gobii* increases rapidly in winter (January, February, March), but the number of these parasites in infested fish remains moderate.

b) In *Z. ophiocephalus*, *H. gobii* is similarly absent in autumn, and prevalence is nil from October to December (Fig. 2a). The parasite first appears in samples collected in January, and the maximum prevalence is observed in May ($P_{MY} = 29.6\%$). The nil prevalence observed in June cannot be interpreted due to the very small number of *Z. ophiocephalus* captured and studied during the course of this month. Apart from the prevalence in June, other variations are confirmed by the fact that at least one of the monthly abundances is statistically different from the others (H_0 rejected with $H = 10.52$, $P < 0.05$, $DF = 4$) (Table I), but the same Kruskal-Wallis test, when applied to mean intensities, does not reveal any difference (H_0 not rejected with $H = 5.09$, $P > 0.05$, $DF = 4$). This parasite is thus absent during the cooling period of the Etang de Thau water; and its presence later becomes regular but species remains rare in infested fish.

c) In *S. cinereus*, *H. gobii* is once again absent in autumn

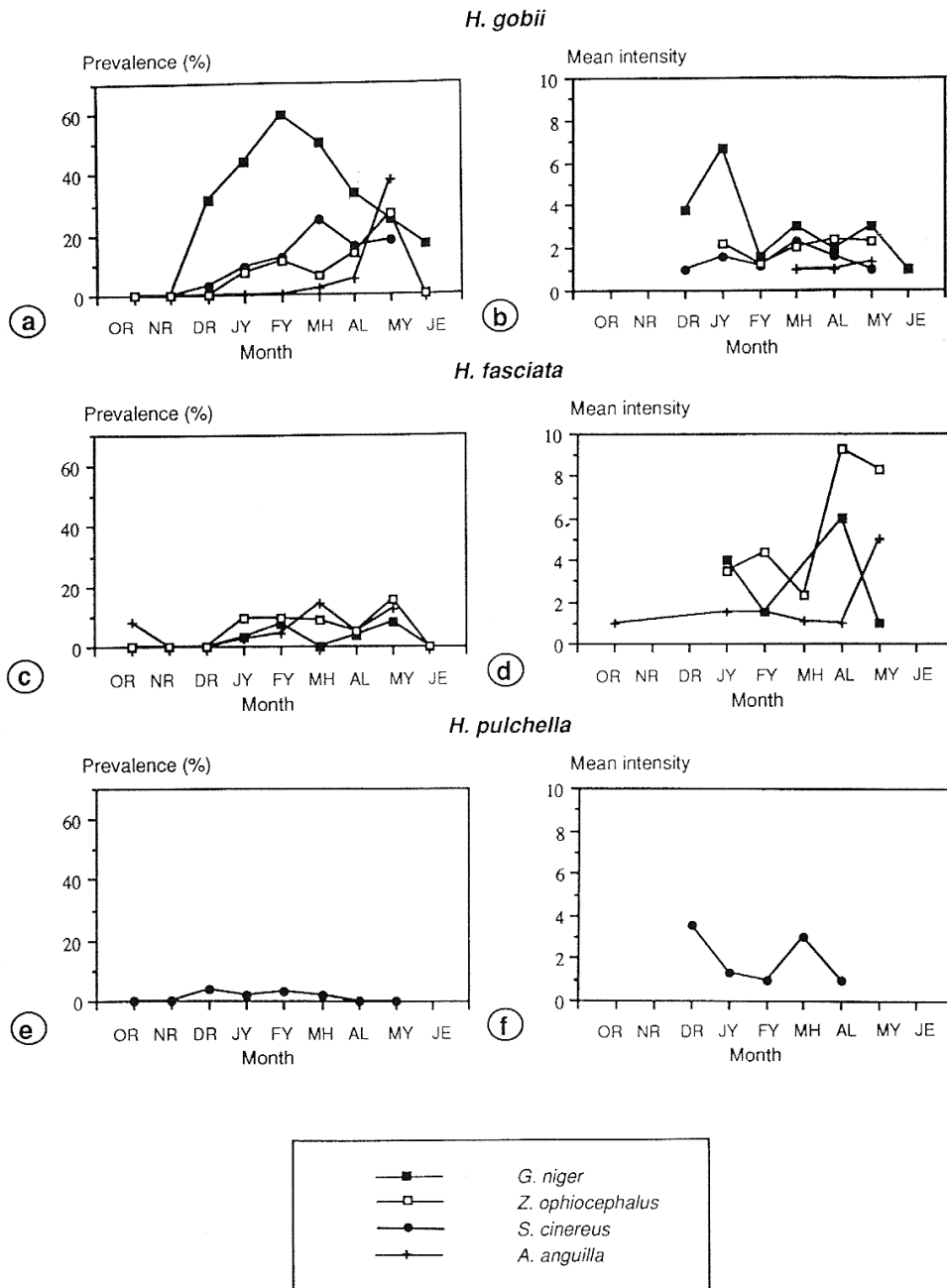


FIG. 2. — Monthly variations of prevalences (a, c, e) and mean intensities (b, d, f).

a : Monthly prevalences of *H. gobii*, in *G. niger*, *Z. ophiocephalus*, *S. cinereus* and *A. anguilla*; b : Monthly mean intensities of *H. gobii* in *G. niger*, *Z. ophiocephalus*, *S. cinereus* and *A. anguilla*; c : Monthly prevalences of *H. fasciata* in *G. niger*, *Z. ophiocephalus* and *A. anguilla*; d : Monthly mean intensities of *H. fasciata* in *G. niger*, *Z. ophiocephalus* and *A. anguilla*; e : Monthly prevalences of *H. pulchella* in *S. cinereus*; f : Monthly mean intensities of *H. pulchella* in *S. cinereus*.
 OR : October, NR : November, DR : December, JY : January, FY : February, MH : March, AL : April, MY : May, JE : June.

(Fig. 2a), and does not appear until December. The prevalences are around 10 % in January and February, and are close to 20 % in March, April and May. If monthly abundances are by consequence significantly different (H_0 rejected with $H = 15.13$, $P < 0.05$, $DF = 4$) (Table I), the same is not true for the mean intensities, which remain stable (H_0 not rejected with $H = 7.84$, $P > 0.05$, $DF = 5$) (Fig. 2b). As in the two gobies, *H. gobic* starts to appear in grey wrasse during winter, then infests about one host in five in spring, but intensities remain low (one or two individuals per host more often than not).

d) In *A. anguilla*, *H. gobic* prevalence (Fig. 2a) is nil in autumn, and in winter up until February. In the period from October to February, this trematode was not found in any of the 152 eels examined. *H. gobic* first appeared in our samples in March, and prevalence increased to reach 37.5 % in May. The Kruskal-Wallis test applied to abundances showed that at least one month differed significantly from the other (H_0 rejected with $H = 14.67$, $P < 0.05$, $DF = 2$); the highest proportion of infested eels in May is the most likely cause of this difference (Table I). On the contrary, the mean intensities (Fig. 2b) of the three months when the parasite is present are not statistically different (H_0 not rejected with $H = 0.67$, $P > 0.05$, $DF = 2$). In other words the number of eels infested by *H. gobic* increases in Spring, but this parasite is only present in these fish in very small numbers, with no monthly variation of intensities.

1.2. *Helicometrica fasciata*

This trematode is present in the two gobies *G. niger* and *Z. ophiocephalus*, as well as in the eel *A. anguilla*. On the other hand, it is not found in the Labridae *S. cinereus*.

a) In *G. niger*, prevalences of this digene are overall much lower than those of *H. gobic* in the same host, only reaching on average 2.33 % (global prevalence) for all of the samples. On the other hand, just as with *H. gobic*, this parasite is absent in autumn; none of the 76 black gobies sampled between October and December were infested by this species. *H. fasciata* appeared in January and continued to be present in very small quantities during the following months, and it was not possible to detect the smallest monthly variation in abundance (Table I) (H_0 not rejected with $H = 0.90$, $P > 0.05$, $DF = 3$). When this digene is present (Fig. 2d), the number of individual parasites per fish is not very different from that already noted with *H. gobic* in the same host. Monthly mean intensities fluctuate between 1 and 6, and there is no statistical difference between them (H_0 not rejected with $H = 3.53$, $P > 0.05$, $DF = 3$).

b) In *Z. ophiocephalus*, the trematode is also absent in autumn (Fig. 2c); prevalence which was determined from 206 grass gobies sampled from October to December is nil. It should be noted that, starting in January, abundances

TABLE I. — Monthly abundance values for *H. gobic*, *H. fasciata* and *H. pulchella* in the different hosts which harbour them (*G. niger*, *Z. ophiocephalus*, *S. cinereus*, *A. anguilla*) (\pm SD).

Parasite	Host	Month									
		OR	NR	DR	JY	FY	MH	AL	MY	JE	
<i>H. gobic</i>	<i>G. niger</i>	0	0	1.2 ± 0.5	2.9 ± 0.9	0.9 ± 0.2	1.5 ± 0.4	0.6 ± 0.2	0.8 ± 0.5	0.2 ± 0.1	
	<i>Z. ophiocephalus</i>	0	0	0	0.2 ± 0.07	0.1 ± 0.05	0.1 ± 0.5	0.3 ± 0.1	0.6 ± 0.2	0	
	<i>S. cinereus</i>	0	0	0.3 ± 0.2	0.1 ± 0.5	0.1 ± 0.04	0.6 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	-	
	<i>A. anguilla</i>	0	0	0	0	0	0.02	0.05	0.5 ± 0.3	-	
<i>H. fasciata</i>	<i>G. niger</i>	0	0	0	0.1 ± 0.1	0.1 ± 0.1	0	0.2 ± 0.2	0.08 ± 0.08	0	
	<i>Z. ophiocephalus</i>	0	0	0	0.3 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	0.5 ± 0.4	1.3 ± 0.7	-	
	<i>A. anguilla</i>	0.08 ± 0.08	0	0	0.04 ± 0.03	0.06 ± 0.04	0.1 ± 0.1	0.05 ± 0.05	0.6 ± 0.6	-	
<i>H. pulchella</i>	<i>S. cinereus</i>	0	0	0.1 ± 0.1	0.1 ± 0.04	0.03 ± 0.02	0.1 ± 0.1	0.01 ± 0.01	0	-	

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remain stable in winter and spring (Table I) (H_0 not rejected with $H = 2.82$, $P > 0.05$, $DF = 4$). The proportion of grass gobies infested does not appear to fluctuate monthly, but certain of these fish are nevertheless more parasitized than others in April and May (Fig. 2d). The Kruskal-Wallis test, when applied to the monthly mean intensities, did not allow us to reject the null hypothesis of intensities equality (H_0 not rejected with $H = 5.39$, $P > 0.05$, $DF = 4$).

c) In *A. anguilla*, *H. fasciata* is rare, but is first observed in samples collected from October (Fig. 2c). This presence in autumn is all the more significant since the number of eels captured and studied from October to December is relatively low (32 individuals). After January, prevalence never exceeds the March maximum of 14 %. The hypothesis of abundances equality cannot be rejected (H_0 not rejected with $H = 7.02$, $P > 0.05$, $DF = 5$). Just as with *H. gobic* in the same host, very low mean intensities were observed, with values being close to 1. There is no perceptible difference between the months (H_0 not rejected with $H = 5.87$, $P > 0.05$, $DF = 5$).

1.3. *Helicometra pulchella*

This digene has an oioxenous specificity as it only infests *S. cinereus*. As with *H. gobic* in the same host, this species is absent in October and November, and first appears in December samples (Fig. 2e). Unlike *H. gobic*, which can achieve prevalences which exceed 20 % (March), *H. pul-*

chella never exceeds 3.5 % (December). Apart from the fact that it is only found in the Labridae, this species is thus very scarce, and in every case is the most rare of the three *Helicometra* species mentioned. It is, naturally, impossible to detect any the slightest variation in abundance between the months (Table I) (H_0 not rejected with $H = 6.41$, $P > 0.05$, $DF = 4$). Intensities fluctuate between 1 and 4 parasites per host infested, these values being very similar to those observed for *H. gobii* and *H. fasciata*. There is no significant variation in monthly intensities (H_0 not rejected with $H = 6.32$, $P > 0.05$, $DF = 4$).

2. ANALYSIS OF THE DEPENDENCE BETWEEN POPULATIONS

The eventual correlation existing between the number of individuals of each congeneric species which are present in the same infracommunities has been analyzed using Spearman's non-parametric coefficient. This dependency between infrapopulation intensities has thus been studied for *H. gobii* and *H. fasciata* in *G. niger*, *Z. ophiocephalus* and *A. anguilla*, and also for *H. gobii* and *H. pulchella* in *S. cinereus*. Results appear in Table II.

TABLE II. — Monthly Spearman's coefficient of rank correlation for the association *H. gobii*/*H. fasciata* parasitizing *G. niger*, *Z. ophiocephalus*, *A. anguilla*, and the association *H. gobii*/*H. pulchella* in *S. cinereus*.

Association	Host	Month					
		DR	JY	FY	MH	AL	MY
	<i>G. niger</i>	-	0.205 n.s.	-0.099 n.s.	-	0.316 n.s.	-0.172 n.s.
<i>H. gobii</i> / <i>H. fasciata</i>	<i>Z. ophiocephalus</i>	-	0.32 *	0.117 n.s.	0.113 n.s.	0.111 n.s.	0.48 *
	<i>A. anguilla</i>	-	-	-	0.345 *	-0.053 n.s.	0.667 *
<i>H. gobii</i> / <i>H. pulchella</i>	<i>S. cinereus</i>	-0.036 n.s.	0.132 n.s.	0.233 *	0.395 *	-0.059 n.s.	-

n.s. : $P > 0.05$.
* : $P < 0.05$.

A) If we first consider the pair *H. gobii*/*H. fasciata*, we are able to observe the following for each host:

a) In *G. niger*, none of the correlation coefficients calculated could be considered to be either negative or positive. Only the value for the month of April is very close to the threshold ($R_s = 0.324$ with $\alpha = 0.05$). This result suggests that colonisation of this teleost by these two *Helicometra* is independent, as indicated by Figures 2a and 2c; in effect it can be observed that the increase in winter and spring of *H. gobii* in *G. niger* does not lead to an increase of *H. fasciata* in the same proportion. This last species is found even more often in *Z. ophiocephalus* and *A. anguilla* than in *G. niger* (Fig. 2c). When *H. fasciata* is present in *G. niger*, Figures 2b and 2d show us on the

contrary that its values are not less than those relating to *H. gobii*.

b) In *Z. ophiocephalus*, only the January and May correlation coefficients can be considered to be statistically greater than 0, even if all the other values are positive. The non-repetitive character of this positive correlation over the course of these months, together with the fact that the values found to be positive are not very different from those of threshold ($R_s = 0.203$ in January and 0.329 in May with $\alpha = 0.05$), have led us to interpret the association between *H. gobii* and *H. fasciata* as being more circumstantial than regular.

c) In *A. anguilla*, the December, January and February coefficients cannot be calculated, since *H. gobii* was not present in this host during this period. Coefficients become significantly greater than 0 in March and May ($R_s = 0.236$ in March and 0.619 in May with $\alpha = 0.05$). Taking into account the very low intensities of *H. gobii* and *H. fasciata* in infested eels (Figs. 2b and 2d), and the occasionally small number of eels sampled (Fig. 1), the increase in these two correlation coefficients is due more to the simultaneous presence of the two *Helicometra* in certain fish than to a linked increase in their intensity in the same hosts.

B) If we turn our attention now to the association between *H. gobii* and *H. pulchella* in *S. cinereus*, most coefficients can be considered to be nil apart from those of February and March. Once again the values found during these last two months are not far from those of threshold ($R_s = 0.208$ in February and 0.213 in March with $\alpha = 0.05$); this should lead us to balance the positive character of these correlations, all the more since *H. pulchella* prevalences are particularly low throughout the year.

Finally, we can deduce that in the case of the three *Helicometra* species, the intensity of one or other associated species are sometimes positively correlated, but only to a small extent. It is also worth noting that none of Spearman's correlation coefficients are significantly negative; this suggests that there is never an increase in intensity of one of the two species without a corresponding decrease in intensity of the other in the same individual host. In most instances there is no monotonous relationship, either increasing or decreasing, between the two quantitative variables studied.

DISCUSSION ET CONCLUSIONS

a) SPECIFICITY AND COMMUNITY STRUCTURE IN THE DEFINITIVE HOST

If one considers the three *Helicometra* species in terms of presence-absence, one notes: 1) that *H. gobii* infests all four teleost hosts, and shows the highest prevalences, at

least in *G. niger*; 2) that *H. fasciata* is present in the two gobies and the eel, but never in the grey wrasse; 3) that inversely, *H. pulchella* only parasitizes the grey wrasse.

H. gobicus is at the same time the most euryxenous species relating to fish, but is also the most common in the four definitive hosts studied. In colonising these four teleosts, *H. gobicus* is the only one of these three species which is in syntopic with *H. fasciata* and *H. pulchella* but never with both at the same time.

b) SPATIAL STRUCTURE AND DENSITY DEPENDENCE

If one considers this problem from a quantitative point of view, the weakness of intensities is quite remarkable: in 97.5 % of cases, intensities are less than 5 individuals. This is not widespread in other trematode communities which live in the digestive tracts of fish, where intensities of several dozen individuals are not rare (Maillard, 1976; Holmes, 1990; Kennedy, 1990). If we now consider the problem using supposed densities (number of parasite individuals per unit of surface, volume, or weight of a tissue or an organ in an infested host) instead of intensities, we then observe the following: the digestive tract of the two gobies is smaller in size than that of the grey wrasse, which in turn is much smaller than that of the eel. In other words, where intensities are similar in different hosts, the density of a species such as *H. gobicus* would in reality appear lower in eels than in grey wrasses, and *a fortiori* than those observed in the two gobies. In practice, the smaller size of the digestive biotope in the two gobies is linked with the highest intensities during certain months, hence density values would be undeniably greater.

In this context, the intervention of a density dependent regulation should lead to more important intensities in the largest digestive biotopes. Since the reverse is true, it is thus difficult to explain the small intensities observed globally by insufficient resources and by the one density dependent regulation. As far as the three trematode populations are concerned, the biotic capacity of these colonized environments (hosts) does not seem to be exceeded. In these biological cycles, a bottleneck restricting the recruitment seems to be situated upstream from the definitive hosts. The moderate prevalences observed in most cases serve to support this argument, as does the fact that the three *Helicometra* are located, without any spatial segregation, in the same part of the digestive tract upstream from the rectum.

Analysis of non-parametric correlation coefficients leads to the same interpretation, since we have shown that there is in the majority of cases an independence between the intensities of species that are simultaneously present, being neither positive (attraction of one species by another), nor negative (exclusion of one by the other).

c) TEMPORAL STRUCTURE OF POPULATIONS

If we now consider the demographic structure of these parasite populations in relation to time, we are able to establish the following observations: 1) apart from *H. fasciata* in eels, the three *Helicometra* species are systematically absent from their respective hosts in autumn; 2) they appear simultaneously in December or January, when the lagoon water at its coldest (Tournier *et al.*, 1982); 3) the three species remain at the same level up until the start of summer, with intensity variations being most often statistically insignificant; 4) during the months when species are present, intra-sample variations are sometimes higher than those of inter-samples. This explains why mean intensities can suddenly increase, whereas corresponding prevalences remain moderate. From an ecological point of view, this explains the accidental appearance of rare individuals which are more parasitized than the average in populations which are globally, slightly infested; this type of distribution gives an account weak overdispersions as previously noted in *Polyopisthocotylea monogeneans* (Silan and Maillard, 1989); 5) it is evident that prevalence variations are all the more important since these species are euryxenous, the two extremes being *H. pulchella* (the rarest species) in *S. cinereus*, and *H. gobicus* (the commonest species) in *G. niger*.

d) FUNCTIONAL DEPENDENCIES BETWEEN CYCLE COMPARTMENTS

All three trematodes studied show a biological cycle which requires three successive obligatory hosts: 1) a fish or definitive host where the digene is found in the adult stage in the digestive tract; this compartment was the subject of this research; 2) a gasteropod or first intermediate host which harbors sporocysts; 3) a necto-benthic invertebrate (probably a small crustacean) or second intermediate host in which cercariae encyst, and then become metacercariae. The biological cycle is completed with the consumption of this invertebrate, and thus of these metacercariae, by the definitive host fish.

Three types of information should be born in mind at this stage of the analysis: 1) Reversat *et al.* (1991b) demonstrated that *H. gobicus*, *H. fasciata*, and *H. pulchella* parasitize respectively, and specifically, the three gastropods *Calliostoma striatum*, *Gibbula adansonii* and *Tricolia tenuis*; 2) furthermore, Reversat and Silan (1991) have shown that these three *Helicometra* have prevalences which are quite similar in their respective molluscs, while *C. striatum* and *G. adansonii* have densities and biomasses which are incomparably higher than *T. tenuis* in the same environment. Decreases in the density and biomass of these three molluscs are most sensitive in summer, even though they are present throughout the year in the lagoon. The recovery of benthic production takes place in autumn, and these

gastropods are also well represented in winter and spring. The three parasites are also present throughout the year, but in winter they are easier to detect; therefore they seem to be better represented in their first intermediate host; 3) finally, using a new experimental transfer technique, de Buron and Maillard (1987), then Maillard and Aussel (1988), have shown that certain *Helicometra* can pass directly from one fish to another due to the predation of one species by another (ichthyophagy), or because of the fairly frequent occurrence of Gobiidae cannibalism (de Casabianca and Kiener, 1969).

These facts lead us to conclude the following remarks and interpretations:

1) summer appears to be globally the least favourable season for these three parasites, even though this period represents a phase of intense feeding for the different definitive host fish species studied. One does not find in the autumn the expected parasite populations in this compartment of the cycle. This may be due to the fact that the second intermediate hosts (invertebrate) which are parasitized, as well as the molluscs, are less abundant during the hottest months. This is also due to the fact that some fish such as gobies experience a significant partial and annual population renewal, with young fish which have not yet been parasitized most commonly found in the autumn population.

2) the three parasites are most represented in their respective molluscs in winter. The emission of cercariae must be amplified at this time of year, in order to explain in the weeks that follow, the incontestable increase in the occurrence frequency of these three *Helicometra* populations in their definitive hosts. There is, admittedly, a large variation between individual hosts. Remember that in spring it is the proportion of parasitized hosts which increases rather than the number of parasites per infested host. The delay between the emission of cercariae out of the molluscs, the appearance of metacercariae in the second intermediate host (crustacean...), and the presence of adult trematodes in teleosts, appears to be fairly short and not to exceed several weeks in the majority of cases. Even though certain periods are more favorable for the progress of these cycles, the relative stability of benthic and necto-benthic communities in the Etang de Thau, a lagoon which is almost marine, explains why these parasites are permanently present in all the compartments of their cycle.

3) if we consider the parasitological flow of these three trematodes in « mollusc » and « fish » compartments, we are able to draw the following conclusions: *Calliostoma striatum*, host of *H. gobii*, and *Gibbula adansonii*, host of *H. fasciata* are two Trochidae which are much more abundant in the Etang de Thau than *Tricola tenuis*, the Turbinidae, host of *H. pulchella* (Reversat and Silan, 1991). Even if the prevalences of these three digenes are globally similar, their mollusc density differences serve to make *H. gobii* and *H. fasciata* far

more abundant than *H. pulchella* on the scale of this lagoon. This element, as well as the fact that *H. pulchella* only parasitizes one teleost species, the grey wrasse, is certainly partly responsible for the lowness of prevalences concerning this digene in its definitive host, as compared to those relating to the two other *Helicometra*. *H. pulchella* has thus fewer potential targets than its congeners as far as gastropods and teleosts are concerned, but this seems to reduce recruitment in fish far more than in molluscs.

With regards to *H. gobii* and *H. fasciata*, eel predation of gobies, or cannibalism which is known to exist amongst gobies, could help to modify the recruitment of these species. It is interesting to note that these two species of *Helicometra* are best represented in their definitive hosts, but are also the only ones where predator-prey relationships are likely to interfere with their biological cycle. This is sufficiently unusual to make it worthy of attention. The part of this process relating to demographic mechanisms does not appear to us to have been quantified. Nevertheless, we have come to realise that the restriction of recruitment in definitive hosts is certainly more a consequence of the demographic « bottle-neck » effect situated upstream. Any favorisation (Combes, 1980) due to rather particular predator-prey relationships does not therefore appear to prevail;

4) our final remarks concern the possible links between the specificity of these digenes, the structure of these different populations, the number of congeners present in different hosts, and the type of speciation which leads to these communities.

Our present understanding is that these three platyhelminths are thus oioxenous with regard to their respective gastropods. *H. pulchella* is similarly oioxenous, whereas *H. gobii* and *H. fasciata* are perfectly euryxenous in relation to their definitive host fish. From a demographic point of view it is thus clear that these three trematodes are even more numerous in their definitive host fish when their specificity is large in relation to this compartment, and when their mollusc is abundant in this lagoon. In other words, there is a direct and complex relationship between the demographic strategies of these *Helicometra* and the nature of their specificity.

Moreover, *H. gobii* and *H. fasciata* occasionally coexist in at least three teleosts, namely the black and grass gobies, and the eel. The coexistence of two congeneric species in the same digestive biotope, moreover with overlapping of spatial niches, poses the problem of the nature of their speciation. Competitive constraints are probably less important in fish than in molluscs. Their diminution, linked with globally low densities, chronic in their definitive host, could well be at the origin of such a differentiation of species. Their speciation could be of a sympatrically synxenic nature (Euzet and Combes, 1980), and once again in direct relation to their demographic strategy.

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