J. Parasitol., 87(5), 2001, pp. 1002–1010

PHENOTYPIC MODIFICATION OF ROACH (*RUTILUS RUTILUS* L.) INFECTED WITH *LIGULA INTESTINALIS* L. (CESTODA: PSEUDOPHYLLIDEA)

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ABSTRACT: In European freshwater, cyprinid fish may be heavily infected by plerocercoids of the pseudophyllidea cestode *Ligula intestinalis* (L.). During their development, these parasites grow rapidly to a large size in the fish's body cavity, characteristically distending the abdomen. In this study, the influence of this tapeworm on roach (*Rutilus rutilus* L.) morphology was analyzed. Forty-five infected and 45 uninfected roach were collected from the Lavernose-Lacasse gravel pit in Toulouse, south western France and examined for 40 morphological measurements to study phenotypic modification of the body and 14 bilateral characters for an analysis of asymmetry. Results indicate that the degree of bilateral asymmetry does not change between infected and uninfected roach, despite the strong host-morphological modifications such as deformation of the abdomen, fin displacements at the level of the tail, and sagging of the vertebral column. The intensity of abdominal distension and fish morphology changes depends on the total parasite biomass present. Differences were observed in morphology at different levels of infection, which relate to established effects of *L. intestinalis* on the physiology and behavior of intermediate hosts. These morphological changes induced by the parasite could increase trophic transmission to the definitive avian hosts.

Many trophically transmitted parasites alter their intermediate host's coloration, behavior, etc. (Holmes and Bethel, 1972; Moore, 1984; Milinski, 1990; Combes, 1991; Poulin, 1998; Thomas and Poulin, 1998; Lafferty et al., 2000). The pseudophyllidean cestode *Ligula intestinalis* (L.) is a widespread and common parasite of cyprinid fish in Europe (Bauer and Stolyarov, 1961), which is known to induce harmful effects in fish (Van Dobben, 1952; Dence, 1958; Wilson, 1971; Harris and Wheeler, 1974; Sweeting, 1976; Kennedy and Burrough, 1981). *Ligula* has been the subject of several studies concentrated on the pathogenicity of the parasite and on its effects on individual fish and host populations (Kosheva, 1956; Arme and Owen, 1968; Wilson, 1971; Garabi and Biro, 1975), but little has been done to quantify the effects on individual fish morphology.

The roach (*Rutilus rutilus* L.) acquires the parasites after consumption of infected copepods; those parasites grow rapidly over several months. They increase from microscopic procercoids to large plerocercoids in the fish's body cavity, characteristically distending the abdomen.

In the present paper, the importance of morphological differences between uninfected and infected roach at different levels of infection is demonstrated using 40 individual phenotypic characters across a set of 90 fish collected in natural conditions. Fluctuating asymmetry estimates were used to determine if the parasite causes host asymmetry, as demonstrated for other organisms (Møller, 1992; Escós et al., 1995; Thomas et al., 1998). Morphological body modification by parasites may potentially disrupt fish stability and swimming capacity, and consequently its ability to escape predators.

MATERIALS AND METHODS

Sampling

Samples of roach were collected from the Lavernose-Lacasse gravel pit located near Toulouse in southwestern France. Fish were collected with a 30-m drag seine with 10-mm mesh size from 21 December 1999 to 14 January 2000. Ninety infested and uninfested fish were sampled and used in parallel to analyze their behavior in experimental conditions. After experimentation, they were deep-frozen for the present study.

Morphometry and bilateral asymmetry

The characters selected included 40 morphological measurements (see Table I) to study phenotypic modification of body condition. Morphological measurements were chosen among all available measurements in the literature (Hubbs and Lagler, 1967; Persat, 1988; Holcík, 1989; Kovác, 1992). As these measurements are all carried out between two distinguishable points, they can be reliably replicated from one fish to another (for example the insertions of different fins). Among these morphological measurements, we have selected bilateral characters (14) (see Table I) for analysis of asymmetry.

A standard protocol for processing each specimen was established. All measurements were made by a single person (G.L.) to minimize observer variation. All characters were measured using a digital electronic calliper to the nearest 0.01 mm. Comparison of 30 consecutive measures of the same character demonstrated that the risk of error is negligible (coefficient of variation, CV = 0.35%). Each fish was weighed to the nearest gram and then dissected. Plerocercoids located in the abdominal cavity were weighed to estimate the total biomass.

Statistical analysis

Because morphological characters strongly depend on body size, we corrected all parameters for host size. Allometry in fish, and more specifically in roach, acts up to a length of 40 mm (Copp and Kovac, 1996). Consequently, the effect of allometry on characters was minimized (Harvey, 1982) by using only subadult and adult fish, with body length between 108 and 158 mm. To determine the effect of parasitic load on fish morphology, a centered principal component analysis (PCA) was used. Since some covariation certainly exists among the 40 morphological measurements and the 14 bilateral characters, PCA techniques are appropriate tools to circumvent the problem of multicolinearity (Ter Braak, 1995). The parametric Student's *t*-test was used to compare uninfected and infected fish. Results were considered significant at the 5% level. For clarity, only the mean (± SD) of the most significant measurements are illustrated.

Fluctuating asymmetry (FA) is a common measure of the small and random differences between the right and the left values of otherwise symmetrical morphological characters (Van Valen, 1962; Palmer and Strobeck, 1986). Pairwise measurements were transformed into signed asymmetry values calculated as the difference between the left (L) and the right (R) sides according to the ratio $(x_L - x_R)/(x_L + x_R)$, with x being the morphological bilateral trait under study (Palmer, 1994). This correction eliminates the problem of bias due to differences between samples in host body size (Ames et al., 1979). To determine the pattern of asymmetry variation, we calculated for each bilateral character the probability that the observed character distribution was normal using a Kolmogorov–Smirnov *D* statistic. Skewness and kurtosis were used to

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Received 17 November 2000; revised 14 February 2001; accepted 14 February 2001.

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TABLE I. List of 40 phenotypic morphological lateral traits and their corresponding codes.

Morphological measurements	Code
Standard length	_Sl_
Postorbital distance	_poO_*
Preorbital distance	_prO_*
Length of head	_lc_*
Upper jaw length	_lmx_*
Head depth (at center of eye)	_hco_
Minimum body depth (least depth of caudal peduncle)	_h_
Distance between dorsal fin base and caudal measuring point	_DC_
Distance between dorsal fin base and pectoral fin base	_DP_*
Distance between dorsal fin base and ventral fin base	_DV_*
Distance between dorsal fin base and anal fin base	_DA_
Horizontal diameter of eye	_Oh_*
Vertical diameter of eye	_Ov_*
Predorsal distance	_pD_
Prepectoral distance	_pP_*
Preventral distance	_pV_*
Preanal distance	_pA_
Distance between pectoral fin base and ventral fin base	_PV_*
Distance between pectoral fin base and fin base	_PA_*
Distance between pectoral fin base and caudal measurement point	_PC_*
Distance between ventral fin base and caudal measurement point	_VC_*
Distance between anal fin base and caudal measurement point	_AC_
Depth of dorsal fin	_hD_
Depth of anal fin	_hA_
Length of pectoral fin	_lP_
Length of ventral fin	_lV_
Length of upper lobe of caudal fin	_lC1_
Length of middle part of caudal fin	_lC2_
Length of lower lobe of caudal fin	_lC3_
Length of dorsal fin base	_lD_
Length of anal fin base	_lA_
Interorbital distance	_io_
Body width at the level of pectoral fin insertion	_laP_
Body width at the level of ventral fin insertion	_laV_
Body width at the level of anal fin insertion	_laA_
Body width at the level of dorsal fin insertion	_laD_
Maximum body width	_la_
Body height at the level of posterior point of head	_HH_
Body height at the level of ventral fin insertion	_HV_
Body height at the level of anal fin insertion	_HA_

* Bilateral characters that have been selected for study of asymmetry.

differentiate between fluctuating, anti-, and directional asymmetry (Palmer, 1994). Significance levels of skewness and kurtosis were calculated according to the method of Sokal and Rohlf (1995).

RESULTS

Infection and host general body condition

Figure 1 illustrates the data obtained using a PCA analysis. The eigenvalues (Fig. 1a) indicate that the axis I (24.07% of total inertia explained) is distinctly more important than axis II (10.45% of total inertia explained). Figure 1b shows the spatial organization of the 40 morphological characters and Figure 1c the organization of the 90 individual fish specimens in the plane defined by the 2 first axes (I and II). The variables _la, laV, laD, laP, PV, PC, pV, HH, HV,_ and _DV_ are negatively correlated with the first axis, whereas _DC, laA,_ and _HA_ are positively correlated with the first axis (Fig. 1b). Other morphological variables as listed in Table I contributed weakly to axes I and II of the PCA. Figure 1c clearly discriminates between 3 groups of fish individuals: (1) uninfected fish specimens, (2) infected fish harboring a parasitic load <5 g, and (3) heavily infected fish with a biomass >5 g. Interestingly, a decrease in parasitic load was explained by the first axis of the PCA (least-square regression, $r = 0.916$, $df = 1, 89$, F-ratio $= 463.65$, and $P < 0.001$).

Figure 2 illustrates the variation of muscle mass across uninfected and infected hosts. We observe a significant reduction in body weight (less parasite) per unit length with the parasite load (results of t-test, $P < 0.001$ between the different levels of parasite load).

Infection and host body width

Differences were found between fish groups in the 3 width parameters, _laP, la,_ and _laA_. Figure 3a and b illustrate the main differences observed between uninfected fish and the 2 categories of infected fish (biomass <5 g and >5 g). Table II summarizes the main results of statistical comparisons between all groups of fish. Differences in host body width for _laP_ and _la_ between uninfected and infected hosts were simply the result of infected fish having their body cavity strongly distorted by plerocercoids. More surprisingly, a decrease in the _laA_ parameter was observed with parasitic load, which should not be directly affected by distortion exerted by larvae on body walls.

Infection and host body height

Two groups of measurement responses were obtained for host body height variation (Fig. 4a, b). First, _HH, HV,_ and _DC_ are different between uninfected fish and infected fish (Table II), but there were no differences between the 2 categories of infected fish. Infected fish have a higher body height at the level of extreme anterior point of head (measured by _HH_), a higher central body height (_HV_), and a shorter distance between the dorsal fin insertion and the caudal fin insertion (_DC_). Second, there were significant differences in _HA_ and _pD_ between the uninfected group and the more heavily infected group and between the 2 categories of infected fish (Fig. 4a, b; Table II). Interestingly, parasites induced a sagging of the dorsum between the dorsal fin base and the caudal measurement point when compared with uninfected specimens of the same length. For the most heavily infected fish (>5 g), the morphological changes are strongly marked by a decrease of body height at the level of the anal fin insertion and a sagging of the dorsum between the head measurement point and the dorsal fin base (Fig. 4b).

Infection and host fin position

The position of fins was considered using 9 measurements, i.e., _pP, PC,_ and _DP_ to measure pectoral fin position, _pV, VC,_ and _DV_ to measure ventral fin position, and _pA, AC,_ and _DA_ for anal fin positions (Fig. 5b). For the _VC_ parameter, no difference was observed. For the _pP, DP, DV,_ and _pA_ parameters, some differences were observed between uninfected fish and infected fish, but not between the 2 categories of infected fish.

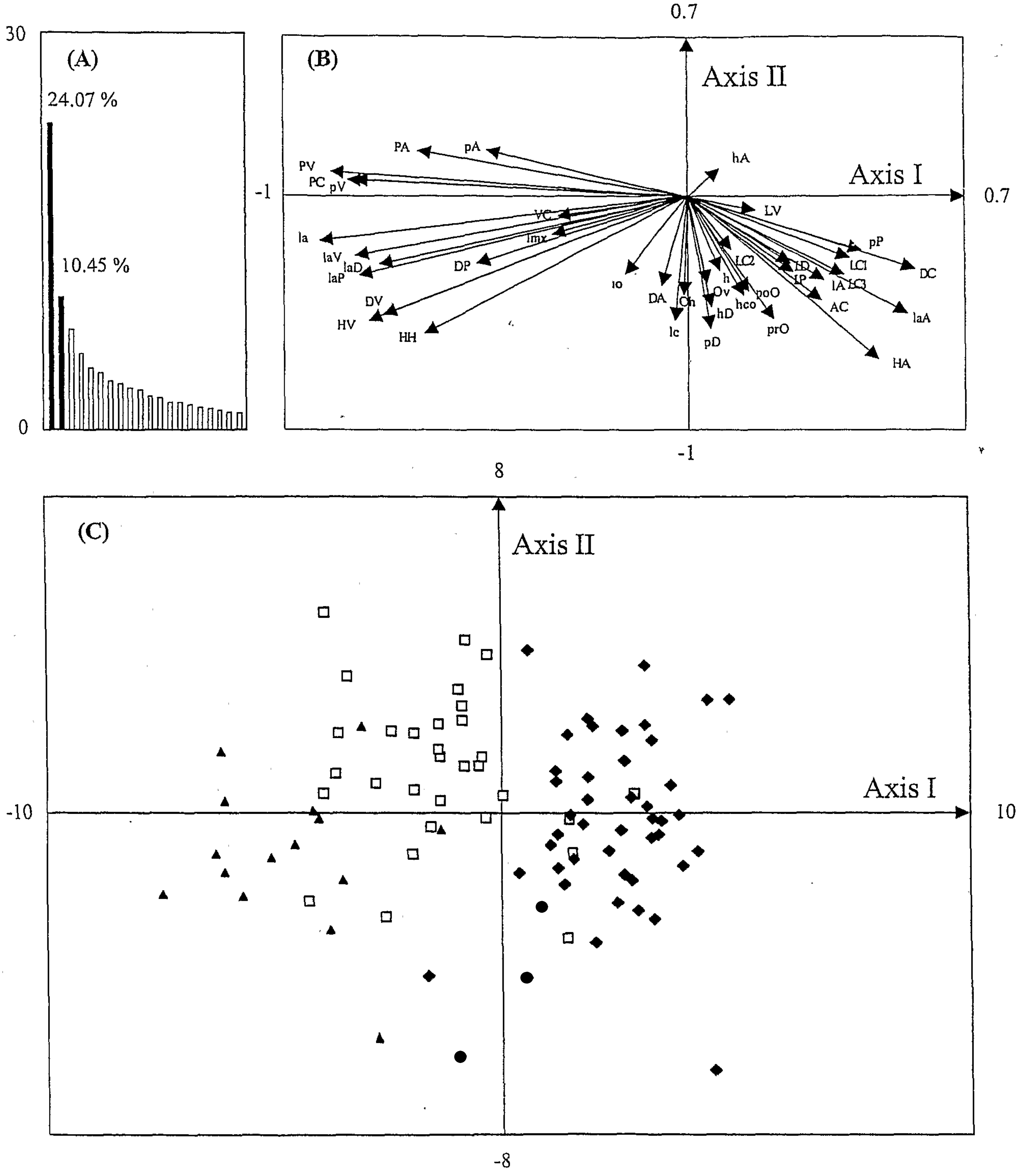


FIGURE 1. Illustration of principal component analysis (PCA) with projection on a plane of the 2 first axis (I and II) resolution. **A.** Histograms of eigenvalue vectors identifying the first two axes contribution (black rectangles). **B.** Projection on the graph of the 39 morphological variables measured across the total set of fish individuals. **C.** Corresponding spatial distribution of fish individuals. PCA analysis discriminates between uninfected fish (◆), infected fish with parasitic load <5 g (□), and infected fish with parasitic load >5 g (▲).

For *PC* and *pV*, differences were found between the 3 categories of fish. Finally, for *DA*, differences were shown between uninfected and weakly infected specimens of hosts, but not between the other categories of fish, whereas for *AC*, no difference was found between uninfected and weakly infected hosts, but differences were seen between the 2 other categories of fish (Fig. 5a). In general, parasitism causes (Fig. 5c) the displacement of the pectoral fin, which moves forward closer to the head, the downward displacement of the ventral fin in accordance with body distension due to parasite larvae, and the dis-

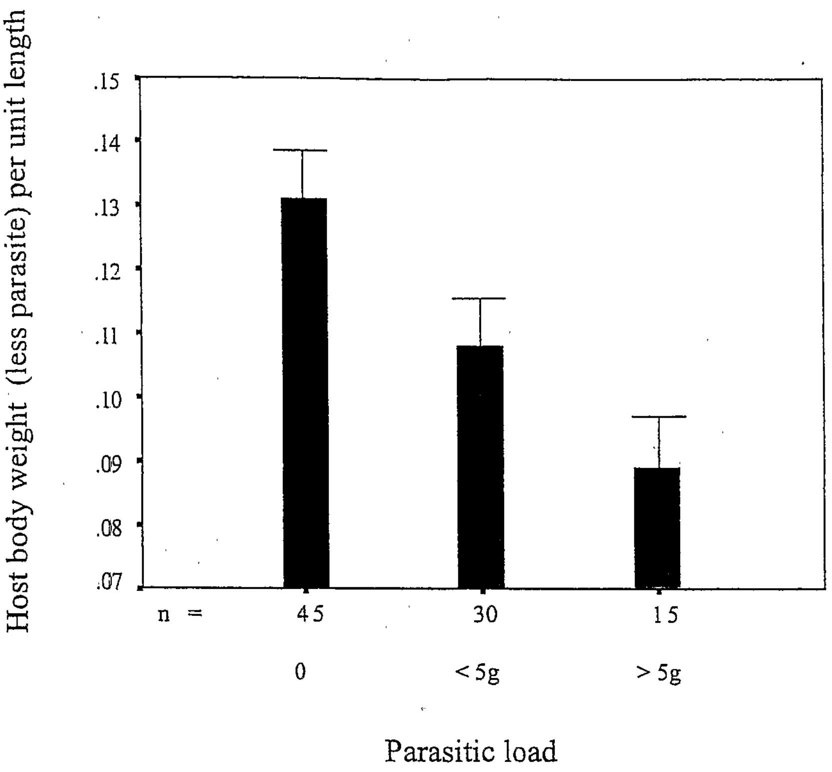


FIGURE 2. Histograms of mean values (± SD) for the host body weight (less parasites) per unit length obtained between uninfected fish (45 specimens) and infected fish with parasitic load <5 g (30 specimens) and >5 g (15 specimens).

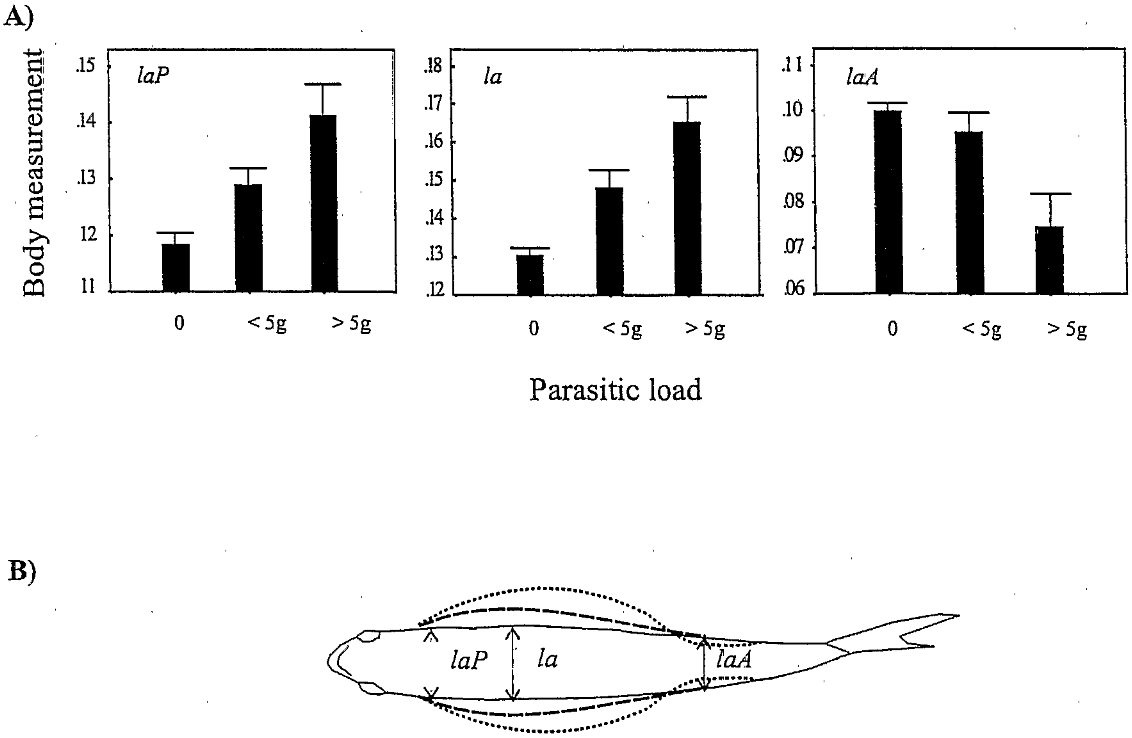


FIGURE 3. **A.** Histograms of mean values (± SD) for the 3 morphological body width characters, i.e., *laP*, *la*, and *laA*, obtained between uninfected fish (45 specimens) and infected fish with parasitic load <5 g (30 specimens) and >5 g (15 specimens). **B.** Graphical representation of body width morphological changes (ventral view) between uninfected control fish and infected fish of the same length. Dashed line represents morphological changes of fish with parasitic load <5 g, and dotted line represents morphological changes of fish with parasitic load >5 g. (Scales on the y-axes differ from figure to figure.)

TABLE II. Pairwise comparisons (*t*-test) of mean morphological variation across 17 traits between different levels of infection in roach. See Table I for explanation on abbreviations used. 0 (uninfected control fish), <5 g (parasitic biomass in fish <5 g), and >5 g (parasitic biomass in fish >5 g).

Morphological measurements	Between 0 and <5 g			Between <5 g and >5 g			Between 0 and >5 g		
	t-value	*P*-value		*t*-value	*P*-value		*t*-value	*P*-value	
laP	−6.164	0.000	***	−4.221	0.000	***	−8.351	0.000	***
la	−7.555	0.000	***	−4.544	0.000	***	−10.932	0.000	***
laA	2.156	0.057	NS	5.101	0.000	***	7.622	0.000	***
HH	−6.667	0.000	***	−0.945	0.352	NS	−6.174	0.000	***
HV	−7.411	0.000	***	−1.687	0.099	NS	−9.522	0.000	***
HA	1.361	0.051	NS	3.958	0.001	***	5.421	0.000	***
pD	−1.362	0.117	NS	2.331	0.028	*	1.109	0.279	***
DC	5.097	0.000	***	0.483	0.634	NS	3.801	0.001	**
pP	4.187	0.000	***	1.925	0.065	NS	5.115	0.000	***
PC	−6.435	0.000	***	−4.912	0.000	***	−11.730	0.000	***
DP	−3.852	0.000	***	−1.218	0.232	NS	−4.485	0.000	***
pV	−5.888	0.000	***	−3.383	0.003	**	−7.237	0.000	***
VC	−1.955	0.054	NS	−0.388	0.702	NS	−1.655	0.112	NS
DV	−6.972	0.000	***	−1.125	0.268	NS	−7.831	0.000	***
pA	−2.906	0.005	**	−2.048	0.052	NS	4.022	0.001	***
AC	0.359	0.721	NS	2.426	0.022	*	2.867	0.009	**
DA	2.342	0.022	*	0.722	0.361	NS	1.516	0.148	NS

NS, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

placement of the anal fin, which moves up in accordance with body height and width decrease.

Infection and host FA

In all 14 bilateral measurements (Table I), FA was observed. This is characterized by a normal distribution of asymmetry values with a mean of about zero (see Table III). No significant skewness or kurtosis deviations were obtained (data not shown). A *t*-test performed on asymmetry characters between uninfected and infected fish indicated no change in bilateral asymmetry despite the importance of morphological changes due to parasitic infection ($P > 0.05$).

DISCUSSION

The presence of *L. intestinalis* plerocercoids has been shown by many workers to be associated with severe pathological effects in fish hosts (see Dogiel et al., 1961; Sweeting, 1976, 1977; Taylor and Hoole, 1989; Wyatt and Kennedy, 1989). In the Lavernose-Lacasse gravel pit in southern France, heavy parasitic loads have been demonstrated, with 30 plerocercoid larvae and a parasite biomass of 7 g (up to 17.5% of the total fish weight) within a single fish. When the parasite development is complete, the worms may occupy the entire host abdominal cavity, characteristically distending the abdomen. The intensity of abdominal distension and fish morphology changes depend on the total biomass of parasite, which exerts significant effects on many aspects of the physiology and behavior of the fish host.

The present study explored the nature of morphological differences in roach with different levels of infestation. We found no asymmetry with respect to paired measures between infected and uninfected fish. Numerous studies have shown that parasites are associated with elevated developmental instability in their host (Møller, 1992, 1995; Polak, 1993; Saino and Møller, 1994; Escos et al., 1995; Folstad et al., 1996), but see Polak (1997) and Thomas et al. (1998) for conflicting views; this phenotypic modification in roach was not seen in the present study. This suggests that plerocercoids do not impair symmetry early in fish development, a time of developmental sensitivity. In fact, if infected young roach were drastically affected by developmental instability, they might be preferentially caught by fish predators, thus disrupting the parasite's life cycle.

However, two types of host phenotype modification were observed. First, some of the host morphological modifications, e.g., deformation of the abdomen and fin displacements, are directly dependent on body wall distension, and are thus merely the result of the accumulation of plerocercoids in fish, i.e., mechanical side effects.

Second, we observed reduced tail width and sagging of the dorsum, causing the back to be somewhat concave from head to dorsal fin and dorsal fin to tail in fish harboring larger numbers of *L. intestinalis* plerocercoids. These differences are not simply a consequence of abdomen distension, but may be better explained by direct physiological effects of plerocercoids on their host. The physiological mechanisms by which such phenotypic modification may be achieved have only recently been investigated (Wedekind and Milinski, 1996; Poulin et al., 1998). Generally, pseudophyllidean worms are known to divert energy from the host, causing an energy drain from nonvital organs of fish (Kuris, 1997; Phares, 1997). Sweeting (1976) considered that infection by plerocercoids may cause muscle atrophy in hosts because of diversion of energy, likely explaining the observed body modification in the present study.

Could these morphological alterations induce a difference in swimming ability between uninfected and infected roach? We

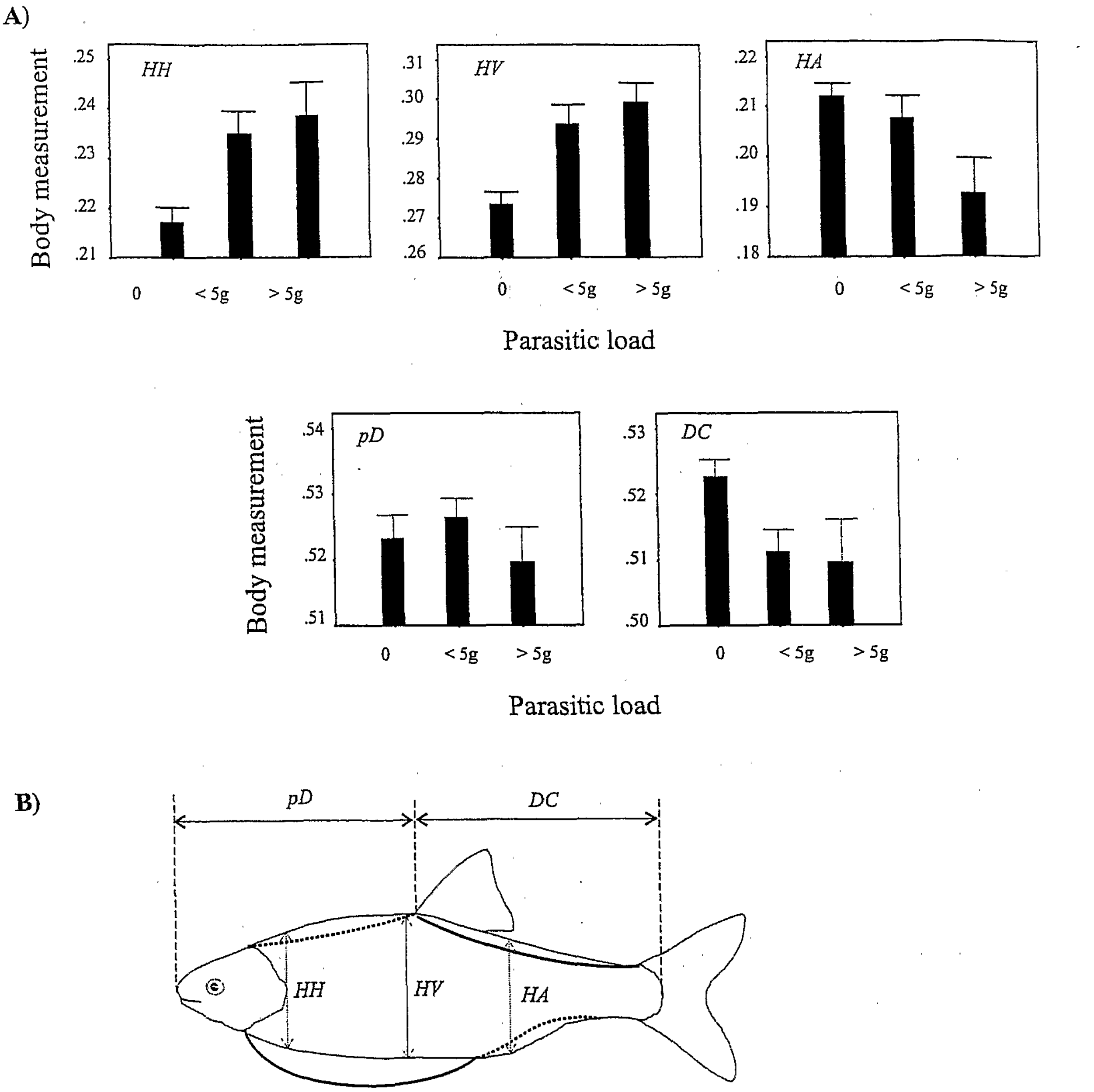
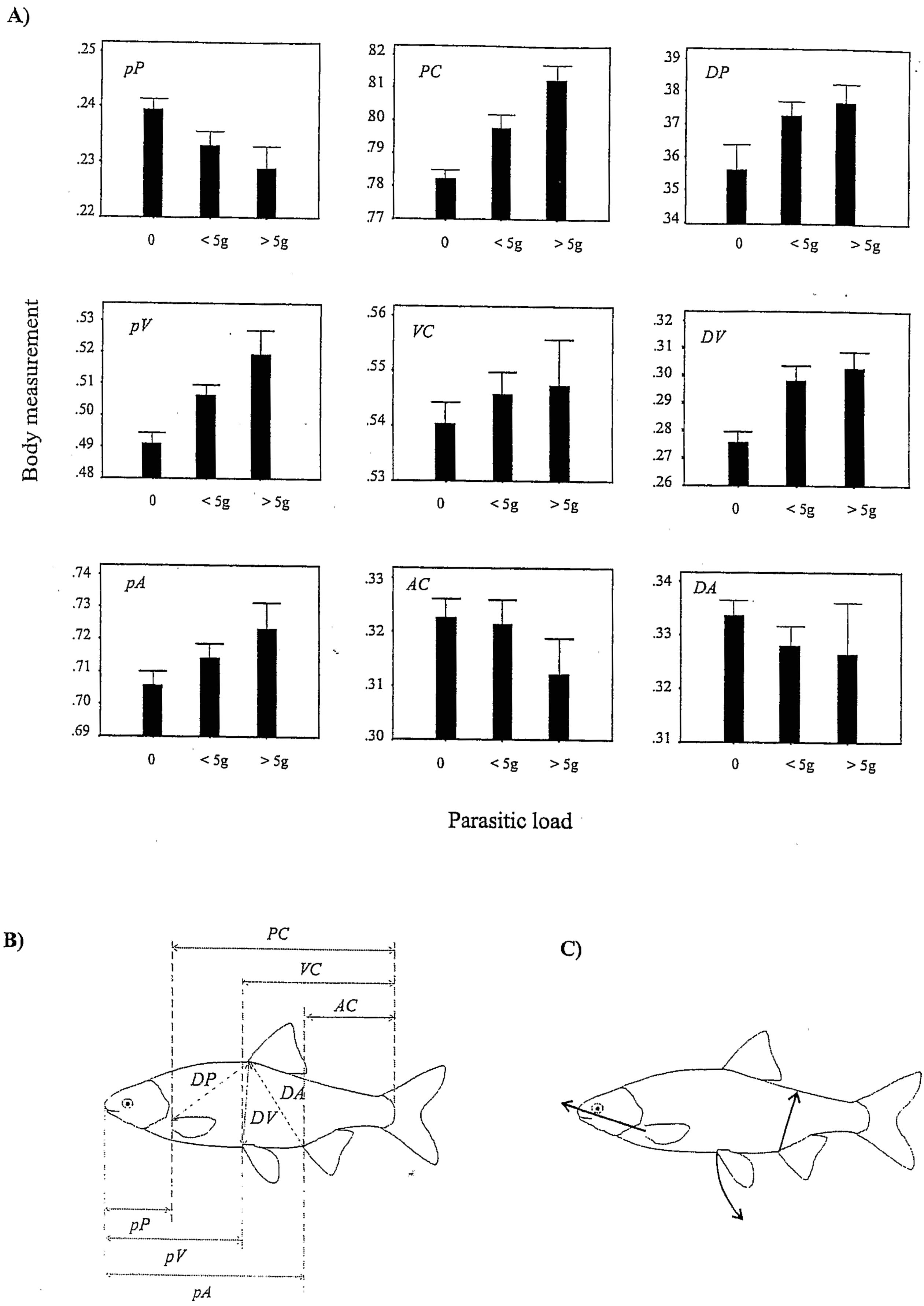


FIGURE 4. A. Histograms of mean values (± SD) for the 5 morphological body height characters, i.e., *HH, HV, HA, pD,* and *DC,* obtained between uninfected fish (45 specimens) and infected fish (45 specimens) with parasitic load <5 g and >5 g. **B.** Graphical representation of body height morphological changes between uninfected control fish and infected fish of the same length. Dark lines represents morphological changes of fish with parasitic load <5 g and >5 g. Dotted line represents morphological changes of fish with parasitic load >5 g. (Scales on the y-axes differ from figure to figure.)

have found differences between the microhabitat used by uninfected and infected fish specimens in natural (Loot et al., 2001) and experimental (Loot et al., unpubl. data) conditions, with more heavily infected roach individuals tending to swim more often near the water surface. Moreover, swimming movements were altered in heavily infected roach (but see Arme and Owen, 1968). It is usually accepted that there is a causal relationship between prey activity and predator attack probability (Wedekind and Milinski, 1996), and certain kinds of movements of the prey seem to act as a sign stimulus for attack by visually oriented predators. Slow movements and erratic swimming by infected roach probably make these prey very conspicuous (see Lafferty, 1997). Their swollen abdomens increase water resistance with a consequent loss of streamlining, together with a loss of camouflage as the ventral side becomes more visible dorsally. The infected roach's preference for shallow waters also may considerably facilitate detection by piscivorous birds. A wide range of parasite-induced alterations in host phenotype have been reported, with a particular emphasis on macroparasites with complex life cycles (Poulin, 1994; Lafferty et al., 2000). A major aim underlying this and related studies is to explore the selective pressures acting on both host and par-


A)
pP
.25
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PC
82
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AC
.33
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.31
.30
DA
.34
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.31
0
< 5g
> 5g
Body measurement
Parasitic load
B)
PC
VC
AC
DP
DA
DV
pP
pV
pA
C)

TABLE III. Means (± SD) of absolute asymmetry values for infected and uninfected roach across a set of 14 symmetrical traits. See Table II for explanation on abbreviations used.

Bilateral characters	Uninfected roach ($\bar{x}$ ± SD)	Infected roach ($\bar{x}$ ± SD)
poO	0.018 (0.017)	0.018 (0.012)
prO	0.029 (0.019)	0.029 (0.021)
lc	0.010 (0.006)	0.008 (0.008)
lmx	0.026 (0.019)	0.026 (0.018)
DP	0.011 (0.027)	0.009 (0.006)
DV	0.008 (0.006)	0.008 (0.006)
Oh	0.018 (0.014)	0.014 (0.010)
Ov	0.020 (0.012)	0.021 (0.016)
pP	0.011 (0.007)	0.010 (0.006)
pV	0.004 (0.002)	0.006 (0.003)
PV	0.010 (0.006)	0.012 (0.010)
PA	0.007 (0.005)	0.008 (0.006)
PC	0.003 (0.002)	0.004 (0.003)
VC	0.006 (0.004)	0.006 (0.005)

asite in the *Ligula*/roach system and, specifically, to test the adaptiveness of the observed parasite-induced host manipulation.

The adaptive host-manipulation hypothesis (see, e.g., Poulin et al., 1998; Lafferty, 1999) asserts that parasites modify their hosts' body or behavior or both to increase parasite fitness. In the *Ligula*/roach system, transmission to the definitive bird host is seen as the key fitness correlate potentially driving adaptive changes to the host phenotype. The challenge in testing the manipulative hypothesis is to reject the simpler 'incidental effect' hypothesis, whereby changes in the host are nonadaptive side effects of parasite infection. To distinguish between these 2 hypotheses, 2 criteria are of central importance, functionality and complexity (Dawkins, 1990; Poulin, 1995). Alterations to the host following parasitism are often strikingly in line with what one would expect to see if the host were to act according to the parasite's interests, suggestive of a purposeful modification. In addition, the mechanism or action of manipulation can be impressively complex on occasion. Taken together, evidence of functional complexity in the effect of a parasite on its host can greatly reduce the parsimony of the 'incidental effect' hypothesis (Dawkins, 1990).

To date, studies on the *Ligula*/roach system have succeeded in illustrating a functional direction to behavioral, and now to morphological, changes in parasitized roach. The course of infection creates changes in shape (this study), habitat selection, and behavior (Loot et al., 2001) that are likely to account for the overrepresentation of parasitized fish in the diet of birds (Van Dobben, 1952), a measure of their accelerated transmission. Two important steps remain. First, the functionality of these changes needs to be assessed in their true currency, e.g., parasite fitness. To do this, the likelihood of avian predation needs to be empirically assessed for the distinct morphological and behavioral states associated with parasitism. Second, the complexity of the parasites' impact on host behavior and morphology requires closer inspection. From a theoretical perspective, progress has been made in exploring the potential existence of a size-dependent manipulative strategy, i.e., only large plerocercoids contribute to manipulation, backed by some tentative statistical support (Brown, 1999). The existence of size-dependent strategies can now be explored in a morphological context, together with other suggested forms of manipulative complexity, notably hormonally mediated manipulation.

Ligula intestinalis plerocercoids have selected an aggressive strategy of exploitation of their hosts, causing important morphological changes in fish, and eventually host death. Thus, it is certain that by reducing the fish's swimming capacity to avoid predation, by modifying a normal swimming behavior, and by conferring to infected hosts a 'chubby-fat' phenotype, the parasite increases the host's vulnerability to predation. It is concluded that roach that are infected with *L. intestinalis* are ostensibly a more profitable prey than noninfected fish.

ACKNOWLEDGMENTS

We thank the team of CESAC at Toulouse for their assistance, and the Ministry of Research and Higher Education for financial support through a research grant offered to G.L. S.P.B. was supported through an ESF grant to visit the CEPM lab, Montpellier, France.

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FIGURE 5. **A.** Histograms of means (± SD) for the 9 fin position parameters, i.e., *pP, PC, DP, pV, VC, DV, pA, AC,* and *DA* obtained between uninfected fish (45 specimens) and infected fish (45 specimens) with parasitic load <5 g and >5 g. **B.** Morphological measurements as used in this study (see Table 1 for abbreviations). **C.** Graphical representation of fin variations between uninfected control fish and infected fish of the same length. (Scales on the y-axes differ from figure to figure.)

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