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ORIGINAL PAPER

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The effects of the ectoparasite *Tracheliastes polycolpus* (Copepoda: Lernaeopodidae) on the fins of rostrum dace (*Leuciscus leuciscus burdigalensis*)

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Abstract Rostrum dace (*Leuciscus leuciscus burdigalensis*) from the River Viaur were found to be infested with the ectoparasite *Tracheliastes polycolpus* (Copepoda: Lernaeopodidae). Samples from five study sites along the river revealed different patterns of parasite infestation. Heavily infested fish were found at the upper study sites whereas much lower infestation levels were observed at the lower study sites. The copepods showed an aggregated dispersion pattern on host fins. The results showed significantly preferred microhabitats, with adult females being more abundant on the anal, pelvic and along the external part of the pectoral fins. The anal and pelvic fins were damaged by the parasite with a loss of their surface area. These fin alterations may reduce the fish's swimming ability and therefore affect the rostrum dace population. Our findings highlight the need to study the effects of parasites on stream fish populations.

Introduction

Parasitism is recognized as a factor that strongly influences animal communities (Anderson and Gordon 1982; Minchella and Scott 1991; Grenfell and Dobson 1995; Combes 1995; Poulin 1998). Parasites may act directly on host survival and demography, or have indirect effects on host physiology and behaviour that interfere with processes such as competition, migration and predation (Price et al. 1988; Thomas et al. 1995; Combes 1996; Poulin 1998). Numerous studies have focused on the pathogenic effects of parasites on natural lentic fish populations (Barber and Huntingford 1995; Lafferty and Morris 1996; Arnott et al. 2000; Loot et al. 2001a, 2001b, 2002) and on fish raised in aquaculture (Gall et al. 1972; Sutherland and Wittrock 1985; McGladdery and Johnston 1988), but relatively few have looked at the consequences of parasite infestation for stream fishes.

In this study, we focused on the lernaeopodid copepod *Tracheliastes polycolpus* (von Nordmann 1832), an ectoparasite on the fins of cyprinid fish. The common host in the River Viaur is the rostrum dace *Leuciscus leuciscus burdigalensis*, but we have also found a few specimens on gudgeon (*Gobio gobio*) and toxostome (*Chondrostoma toxostoma*). The adult female *T. polycolpus* is anchored to host fins and feeds on the epithelial cells and mucus of the host, characteristically raising blisters on the fin surface (Fryer 1982).

T. polycolpus has been the subject of several studies dealing mainly with parasite morphology and systematics (Fryer 1982), host-parasite records (Silfverberg 1999) and geographic distribution (Gurney 1933; Aubrook and Fryer 1965; Fryer 1982; Silfverberg 1999). However, there is currently no information about the exact role played by this parasitic copepod in fish populations, something which is essentially due to the lack of field information on the relative importance of such parasites in ecosystems and their regulatory impact on host populations.

This paper describes the host-parasite interactions between *T. polycolpus* and rostrum dace in the River Viaur. The rostrum dace is a subspecies of dace, endemic to south-western France (Spillmann 1961; Chappaz et al. 1998) and previously classified as 'vulnerable' by Lelek (1987). In the River Viaur, an important decline in dace abundance has occurred since the 1950s (Poulet, unpublished data). The causes of this decline are various, but modification of the river's natural course (construction of weirs and dams) and pollution seem to be the most obvious.

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The aims of this study were: (1) to study the distribution of *T. polycolpus* in five study sites along the River Viaur and among different fin microhabitats within one host species, the rostrum dace; (2) to quantify the magnitude of the pathogenic effects exerted by this crustacean parasite on the different fins; and (3) to discuss its impact on the rostrum dace population within the context of biological conservation.

Materials and methods

Study area and sampling sites

The River Viaur is located in the Adour-Garonne basin (south-western France) (Fig. 1). This rain-fed stream has its source at an altitude of 1,090 m in the Piedmont zone of the Massif Central mountains. Its confluence with the River Aveyron is situated 169 km downstream, at an altitude of 150 m. The fish community of the river comprises 18 species belonging to the following families (Poulet, unpublished data): Cyprinidae (12 spp.), Balitoridae (1 sp.), Esocidae (1 sp.), Percidae (2 spp.) and Salmonidae (2 spp.). For the purpose of this study, we selected five sampling sites—Bannès, Albinet, Ayres, St Just and Calquière—along approximately 60 km of stream (Fig. 1). No change was observed in the fish community composition between the five sampling sites. Minnow, gudgeon and toxostome dominated the community (unpublished data).

Fish sampling

A total of 147 rostrum dace were collected from Bannès (24 specimens), Albinet (29 specimens), Ayres (25 specimens), St Just (27 specimens) and Calquière (42 specimens). Collections were made using electric-fishing in the summer of 2003. The power source used was a DEKA 7000, generating 200–500 V with an intensity range of 1–3 A. After capture, the fish were anaesthetized and measured to the nearest millimetrr (total body length).

Parasite analysis

Levels of parasitic infestations were assessed using epidemiological parameters such as prevalence and intensity of infestation (Margolis et al. 1982; Bush et al. 1997).

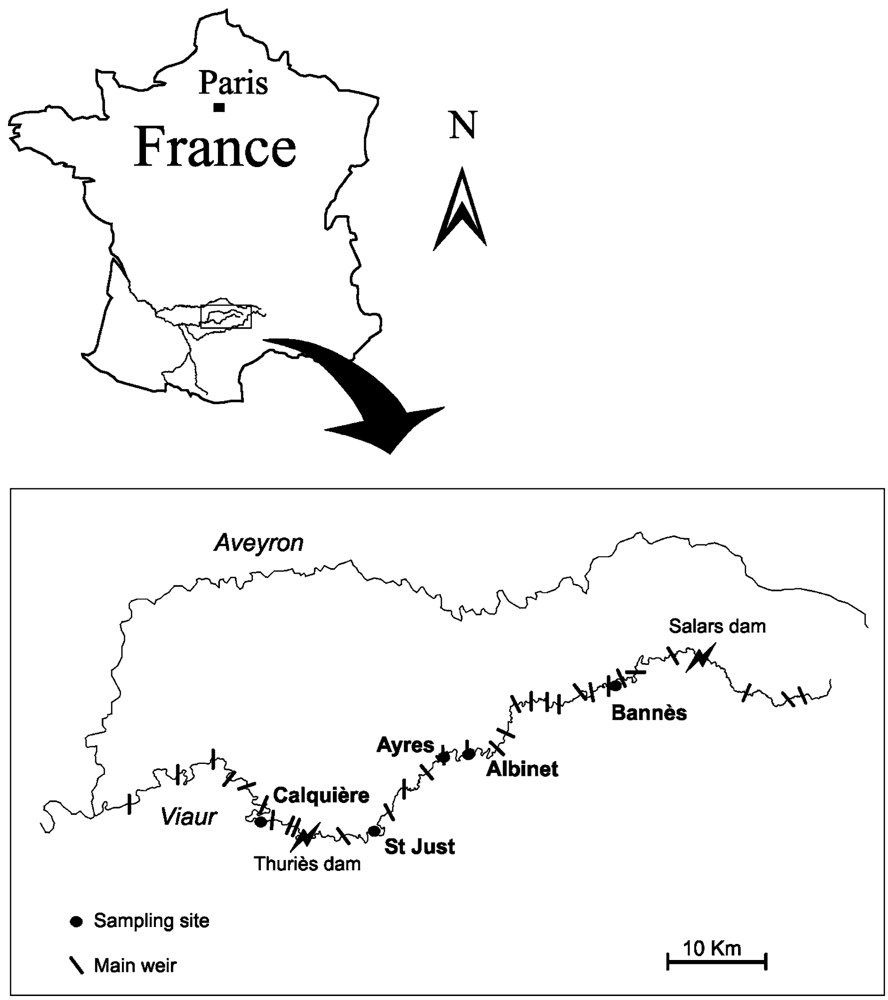

Fig. 1 Map of the River Viaur basin showing sampling sites. The *lines* indicate the position of the main weirs

We used parasite aggregation as a measure of microhabitat preference. Aggregation was measured according to Ives (1988, 1991) and Šimková et al. (2001). It was expressed as J, which measures the proportional increase in the observed number of conspecific parasites relative to a random distribution when fins were considered as independent patches.

$$J = \frac{\sum_{i=1}^{p} \frac{n_i(n_i-1)}{m_1} - m_1}{m_1} \quad (1)$$

where n_i is the number of *T. polycolpus* on fin i, m_1 is the mean number of *T. polycolpus* per fin and p is the number of microhabitats ($p=16$). A value of $J=0$ indicates that individuals are randomly distributed, while a value of $J=0.5$ indicates an increase of 50% in the number of parasites that occur on the same patch (e.g. fin) above a random distribution.

The spatial distribution of *T. polycolpus* on rostrum dace was analysed. For this purpose, the position of each individual parasite was recorded on 16 different microhabitats: caudal-left, caudal-right, dorsal-left, dorsal-right, pectoral internal side-left, pectoral external side-left, pectoral internal side-right, pectoral external side-right, pelvic internal side-left, pelvic external side-left, pelvic internal side-right, pelvic external side-right, anal-left, anal-right, skin-left and skin-right. As these 16 microhabitats had different surface areas, we determined the numbers of copepods per cm^2 of fin/skin.

To estimate the effect of *T. polycolpus* on dace fins, a picture of the left and right sides of each dace was taken with a digital camera. The camera was fixed on an L-shaped bracket to keep the same axis of view for all fish and a metric ruler was placed alongside the fish to provide a baseline scale. The same focal length was kept in order to avoid any picture distortion. Fish fins were held spread with fine needles. We used the ImageTool software (free download at http://ddsdx.uthscsa.edu/dig/itdesc.html) to measure the area of each fin. Rostrum dace were released back into the water because we did not want to alter the local population inside these study sites.

Statistical analysis

To compare the mean parasite intensity among the five study sites, we used analysis of variance (ANOVA). Data were log $(x+1)$ transformed in order to meet the ANOVA assumptions of normality and homoscedasticity. We used a Tukey multiple comparison test to establish the pattern of differences among sites. The parasite prevalence among the five study sites was compared using a chi-square test (Zar 1999). For multiple comparisons tests, significance levels were Bonferroni adjusted (Zar 1999).

To compare the number of parasites observed between different fin microhabitats, we used a Student's t-test (Zar 1999). Data were log $(x+1)$ transformed in order to meet the t-test assumptions of normality and homoscedasticity.

To quantify the impact of parasites on fin surfaces among the five study sites, we first determined the existing relationship between the fin area and the total fish length of unparasitized fish. Based on the equation associated with each curve, we then calculated the expected area of each fin for infested fish and compared it to the observed areas. A high coefficient of determination between expected and observed values ($R^2>0.5$) indicated that the observed fin area was close to that obtained for unparasitized fish, and therefore that parasite impact on fins was very limited or non-existent. In contrast, a low coefficient of determination ($R^2<0.5$) indicated an impact of the parasites on the fin area, the degree of which was given by the value of the coefficient of determination.

Statistical analyses were performed using SPSS release 8 for Windows (Norusis 1993).

Results

Parasite identification and description

Examination of the fins and body surface of 147 rostrum dace revealed the presence of 1,463 parasitic copepods identified as *T. polycolpus*. Individuals were differentiated by examination of both the cephalothorax and trunk which are elongate and tubular (Fryer 1982). All copepods were sexually mature females with 5.49 ± 0.36 mm (mean ± SD) in total body length (range 5.06–6.33). All were attached to the host with a wide, disk-shaped bulla that was 0.26 ± 0.03 mm in diameter (range 0.21–0.33). Most females had two egg sacs that were 3.63 ± 0.45 mm long (range 2.66–4.26) and each sac contained 113 ± 34.47 eggs (range 40–164), 0.21 ± 0.01 in diameter (range 0.19–0.27).

Distribution of infection

The five study sites on the River Viaur had different patterns of parasite infestation by *T. polycolpus* (Table 1). In three study sites—Bannès, Albinet and Ayres—individual dace were heavily parasitized with *T. polycolpus* as shown by the high values of the epidemiological parameters prevalence and mean intensity (Table 1). Parameters of infection were not significantly different between the three sites. The highest number of parasitic copepods found on a single host was 61 at Bannès. In Bannès, Albinet and Ayres, *T. polycolpus* displayed an aggregated dispersion pattern on host fins (Table 1). Parasitic infection was very low for hosts collected at St Just and Calquière (Table 1), and these sites did not differ significantly from each other. At these sites, the highest number of parasitic copepods found on a single host was two at St Just.

Table 1 Number of fish, fish lengths (mean ± SD, range in parentheses), parasite prevalence, parasite intensity (mean ± SD) and aggregation of *Tracheliastes polycolpus* on rostrum dace caught in the River Viaur in July and August 2003

Locality	Number of fish ± SD	Fish length (mm) ± SD	Prevalence (%)	Intensity of infection	Aggregation ± SD
Bannès	24	268 ± 19.1 (242–299)	95.8	19.3 ± 15.1	33.1 ± 26.1
Albinet	29	235.9 ± 27.5 (154–273)	96.5	15.1 ± 9.2	22.1 ± 12.6
Ayres	25	241.2 ± 28.4 (185–315)	96.0	24.1 ± 14.2	16.8 ± 8.1
St Just	27	226.6 ± 35.1 (155–280)	44.5	1.2 ± 0.4	-
Calquière	42	201.5 ± 38.2 (104–300)	42.8	1	-

Fish total length differed markedly among the study sites (Table 1) (F = 17.395, df = 4, 136, P < 0.001). Fish collected from Bannès were significantly larger than at any other site (Tukey test, P < 0.05) and fish from Calquière were significantly smaller (Tukey test, P < 0.05). There was no significant difference between the three other sites.

Microhabitat preference

Most adult female *T. polycolpus* were recovered from fins; however, dace on which the fins were heavily infested often had a few adult females attached to the body surface. Of the 1,463 adult copepods found, 94.2% (1,378/1,463) were attached to the fins and only 5.8% (85/1,463) were attached to the body surface. When the number of copepods present on a fish was very low (one to two individuals per fish), 60% were attached to the external pectoral fins, 20% to the anal fins, 15% to the pelvic fins, 5% to the skin. *T. polycolpus* was never found on the caudal or dorsal fins.

The distribution of adult female copepods among the fins and body for the three study sites Bannès, Albinet and Ayres is shown in Fig. 2. Most of the copepods were found on the anal, pelvic and pectoral fins whereas there was no preference for attachment to either the left or the right side.

With respect to parasite intensity for each side of the paired fins, *T. polycolpus* appeared to select an attachment site on the external part of pectoral as opposed to the internal part of these fins (t-test, P < 0.001) (Fig. 2). We also found a significant preference for attachment on the external part of pelvic fins in dace from Albinet (t-test, P < 0.05) (Fig. 2b).

Pathogenic effects

Observations on rostrum dace heavily parasitized by copepods showed the fins to be haemorrhagic. A comparison of infested and uninfested fish showed the damage to the fins to be very clear, with the almost total destruction of some fins (Fig. 3). The maximum destruction of fin surface area (R^2 < 0.5) was noted on the anal and pelvic fins at Bannès, Albinet and Ayres (see Fig. 4d, e). Moreover, the dorsal and pectoral fins were damaged in dace from Bannès (respectively R^2 = 0.1554 and 0.3196).

The value of the determination coefficient was high for the caudal fins (R^2 > 0.7337), showing that these were less susceptible to copepod damage (Fig. 4a).

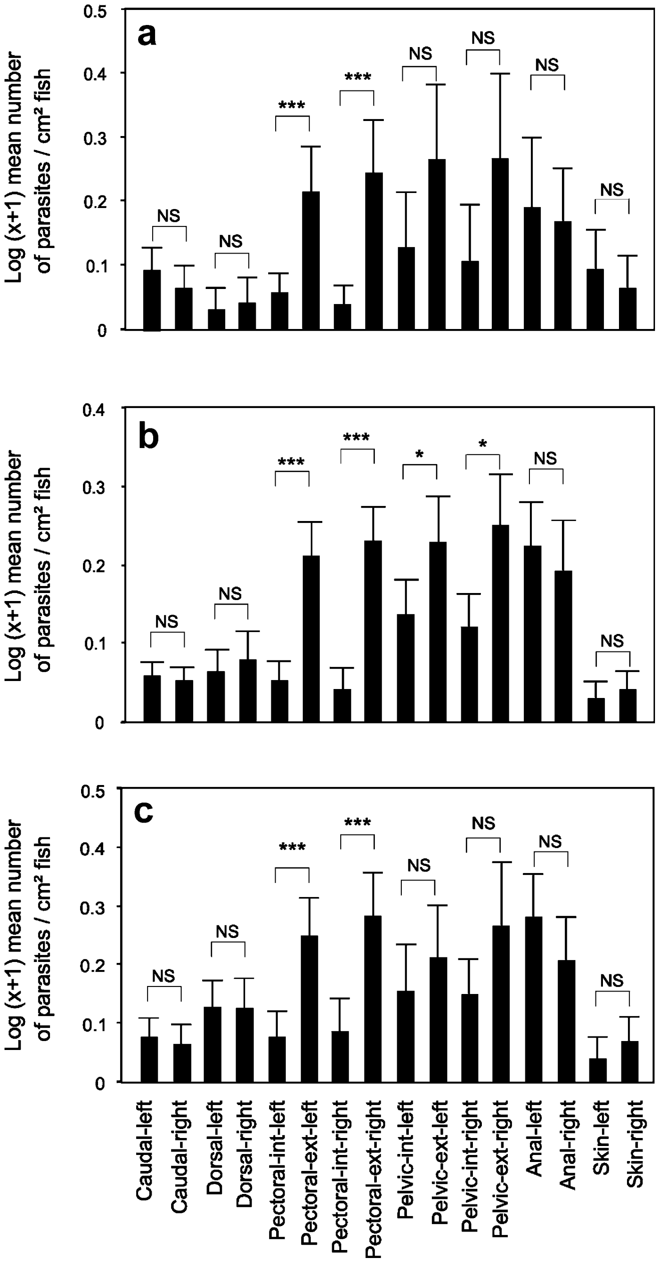

Fig. 2a–c Log (x + 1) mean number of parasites per cm^2 fish (± SD) on the different microhabitats of rostrum dace. **a** Bannès, **b** Albinet and **c** Ayres. *** P < 0.001, * P < 0.05, *NS* not significant

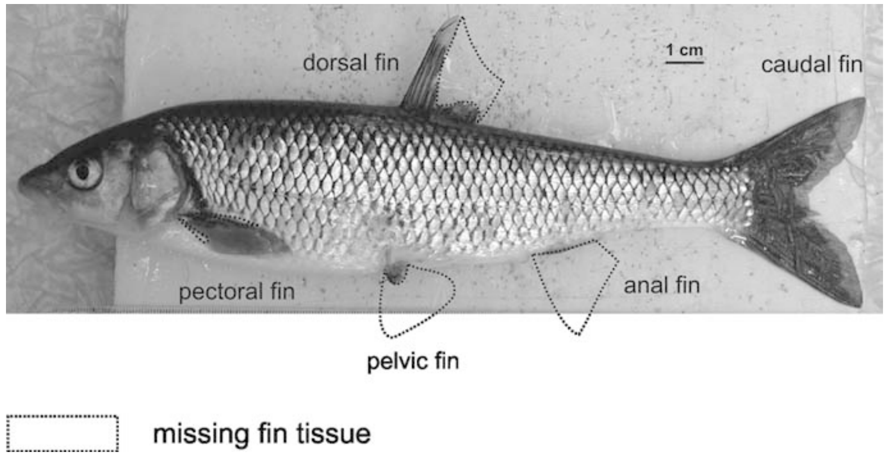

Fig. 3 Fins of a heavily parasitized rostrum dace from Bannès showing tissue damage caused by adult female *Tracheliastes polycolpus*

Figure 5 shows alteration levels for the different fins based on the value of the determination coefficient at Bannès, Albinet and Ayres. No fin alteration was observed from St Just or Calquière ($R^2 > 0.6653$).

Discussion

Distribution of infection

T. polycolpus is widely distributed in the northern Paleartic region. It was found for the first time in several European countries in the 1930s (Fryer 1982). This study represents the first report of *T. polycolpus* infecting rostrum dace in France.

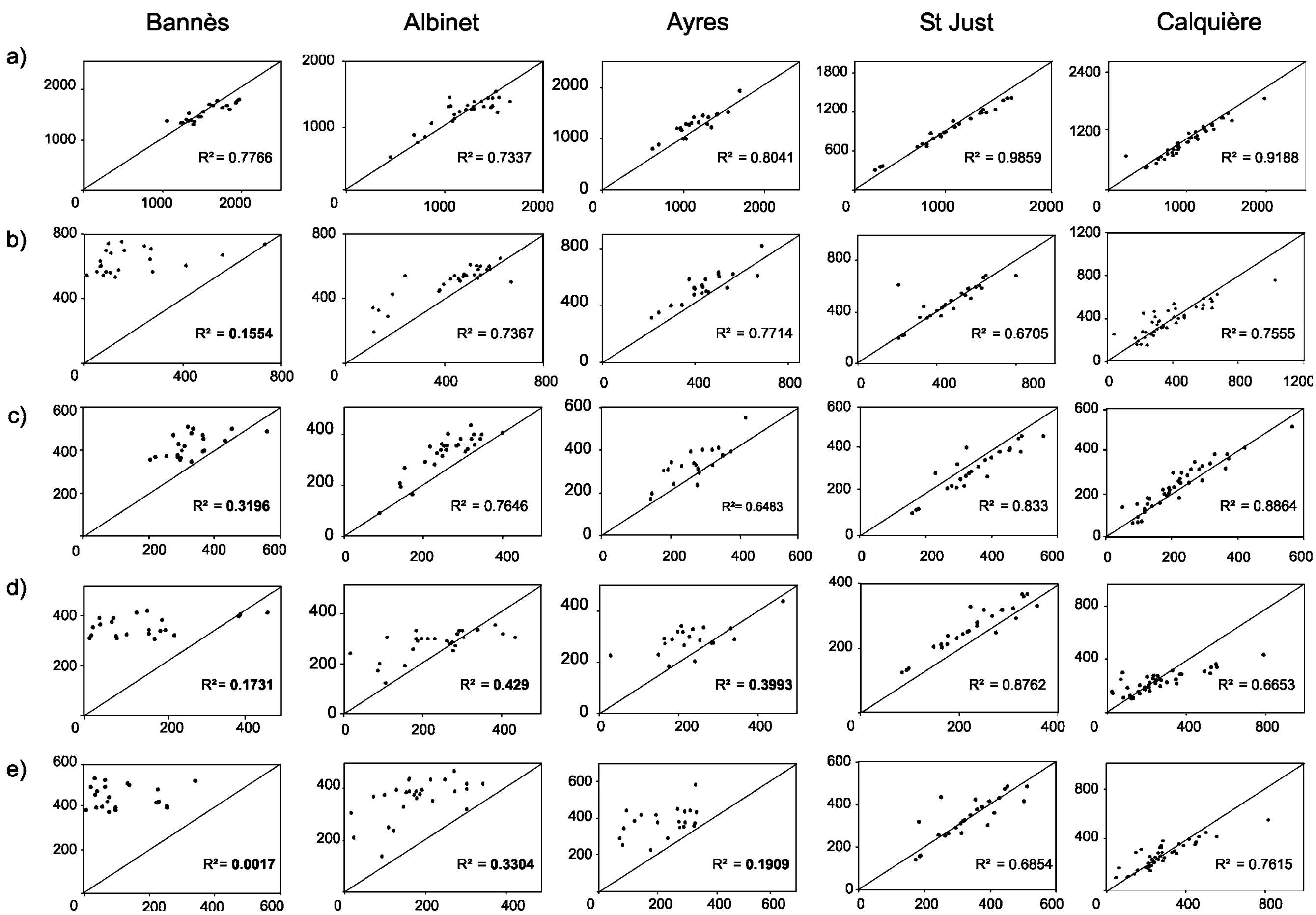

Fig. 4a–e Relationship between the observed and the estimated values of the fin area in Bannès, Albinet, Ayres, St Just and Calquière. **a** Caudal fin, **b** dorsal fin, **c** pectoral fin, **d** pelvic fin and **e** anal fin. $R^2 < 0.5$ are indicated in *bold*, showing fins with copepod damages

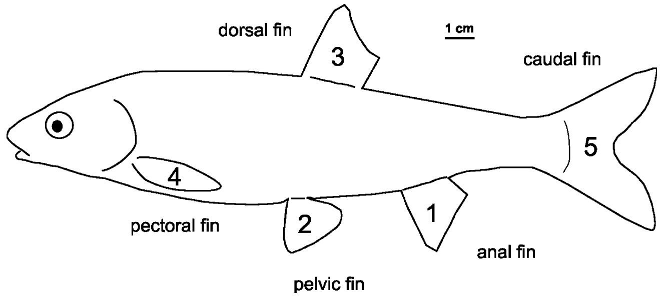

Fig. 5 Alteration level of the different fins of rostrum dace based on the value of the determination coefficient [from 1 (more altered) to 5 (less altered)]

The heavy *T. polycolpus* infestations (maximum 61 copepods) reported in this study approach the heaviest copepod infestations found in previous fish surveys. For instance, Fasten (1921) and Black (1982) observed 61–250 adult female copepods, *Salmincola edwardsii* (Copepoda: Lernaeopodidae), on wild populations of adult brook trout (*Salvelinus fontinalis*).

All copepods seen were sexually mature females. Indeed, males of the family Lernaeopodidae are ephemeral dwarfs, usually dying very soon after mating and consequently very difficult to find (Kabata 1986).

In the present survey, most *T. polycolpus* collected were found on dace from Bannès, Albinet and Ayres. Relatively few were observed on fish taken at St Just and Calquière. Differences in parasite load on dace among sites could be related, but not exclusively, to different prevailing environmental conditions. Indeed, different patterns of parasite infestation may occur in response to environmental parameters such as temperature, water flow and/or oxygen level. For instance, the life span of *Lernaea cyprinacea* (Copepoda: Lernaeidae) is modified by temperature. In Japan the parasitic adult phase was found to last 4 weeks at 27°C but 5 or 6 months during the cold winter period (Kasahara 1962). Thus, the life cycle of *T. polycolpus* could be facilitated in the upper study sites at Bannès, Albinet and Ayres due to a lower prevailing temperature. Moreover, since the 1950s, weirs and dams have been built along the Viaur River, which may have influenced fish migration and environmental conditions, and induced different patterns of parasite load along the river.

Biological factors, such as the distribution of the hosts, may also influence the level of infestation. According to Bowen and Stedman (1990), the prevalence of *Salmincola corpulentus* (Copepoda: Lernaeopodidae) on bloater (*Coregonus hoyi*) depends on the presence of suitable hosts during the critical infective stage. Although the total length of fish from Bannès and Calquière differed significantly from the other study sites (the largest fish were present in Bannès and the smallest in Calquière), the length frequency distributions at the five locations do not seem to account for the differences in parasite load observed (Table 1).

Microhabitat preference

It is known that parasites are aggregated among their habitat patches, i.e. they are generally found aggregated among different host species (Poulin 1993; Morand et al. 1999) or among individual hosts within a host population (Shaw and Dobson 1995; Šimková et al. 2000). In this survey, we calculated parasite aggregation within hosts considering the different fins as individual patches. The aggregation among different microhabitats was recently investigated by Sasal et al. (2000) for digenean endoparasites within the digestive tract of sparid and labrid fishes, as well as by Šimková et al. (2001) for ectoparasites (Monogenea: *Dactylogyrus*) on the gills of roach (*Rutilus rutilus* L.).

Our results show that *T. polycolpus* had an aggregated distribution on host fins. In particular, we found that it was more abundant on the anal and pelvic fins. Anal and pelvic fins are skin fins (Videler 1993) and this structure may facilitate the anchoring of copepods. We also found more copepods on the external part of pectoral fins than on the internal part. Indeed, the resting position (pectoral fins close to the body) probably prevents the anchorage of the parasites on the internal part. On the other hand, the external part of the pectoral fins may provide a more suitable substrate that meets the requirements for permanent anchoring and development of copepods.

When the parasite intensity was very low, 60% of copepods were attached to the external side of pectoral fins; *T. polycolpus* were never found on caudal and dorsal fins and were relatively scarce on the body surface of fish. Thus, the external pectoral fins constitute a primary site of attachment for *T. polycolpus*.

The results of microhabitat preferences have been reported for other copepod-fish associations. For instance, Sutherland and Wittrock (1985) observed that adult female *Salmincola californiensis* usually attached to the distal ends of the gill filaments or to the gill bars of farm-raised rainbow trout, *Oncorhynchus mykiss*. Bowen and Stedman (1990) found that the dorsal anterior portion of the branchial rim of bloater, *C. hoyi*, was the preferred site of attachment of sexually mature females *S. corpulentus*.

Pathogenic effects

Lernaeopodids may affect their hosts through pathological effects, sometimes causing slight inflammation where the bulla is inserted into the host, but most damage is caused by the rasping action of the mandibles (Fryer 1982). Our results show that rostrum dace infested by *T. polycolpus* present obvious damage to their anal and pelvic fins leading to the almost total destruction of these fins in Bannès, Albinet and Ayres. Different deleterious effects observed across fins are probably the result of both the degree of infestation and differential fin sensibility. Indeed, skin fins, such as the anal and pelvic fins (Videler 1993), should be easily damaged.

The genetic structure of the host population could also be altered by river fragmentation and thus have repercussions on individual fitness. Indeed, the fins of dace specimens found at the upper study site of the river (Bannès) were more altered than the fins of dace found at the lower study sites (Albinet and Ayres), although the parasite load was similar in the three sites. This may be explained by the fact that the upstream populations are isolated by numerous weirs that prevent upstream migration and allow only downstream movement (Poulet, unpublished data). Furthermore, due to the proximity of the dams that reduce water flow and enhance silting of the spawning ground, these populations are small. Thus, these small isolated populations may be subject to a high level of inbreeding that may reduce their capacity to resist parasitic infection (Hedrick et al. 2001; Arkush et al. 2002).

Kabata and Cousens (1977), Sutherland and Wittrock (1985) and Nagasawa and Urawa (2002) have also reported tissue destruction caused by adult *S. californiensis* on salmon (*Oncorhynchus masou*) with the loss of 25% of the total gill surface. Damage resulting from the presence and activity of *T. polycolpus* on the host may be the result of mechanical side effects. According to Kabata and Cousens (1977), the structure and function of appendages used by *S. californiensis* for feeding induce the atrophy and eventual disappearance of the distal portions of gill filaments. However, these alterations are not simply a response to the attachment and activity of copepods, but may also be explained by the direct physiological effects of *T. polycolpus* on their host. Indeed, Friend (1941) and Sutherland and Wittrock (1985) found that the major reason for the indentation of salmon and trout gill filaments was the inhibition or slowing down of filament growth owing to the diversion of blood from the filament to the copepods.

Fins are used for movement, stability, spawning, and as tactile organs (Lindsey 1978). Damage caused by heavy copepod infestation may render fins non-functional.

Indeed, pelvic and anal fins play an important role by acting as stabilizers to prevent the fish from rolling as it moves through the water, and the single dorsal fin serves to help balance the fish while swimming (Lindsey 1978; Drucker and Lauder 2001, 2003). Pectoral fins are actively recruited for a variety of manoeuvring behaviours, including hovering, low-speed turning and rapid deceleration of the body during braking (Drucker and Lauder 2003). Consequently, pelvic, anal, dorsal and pectoral fin erosion may reduce the fish's swimming ability. For most animals, stability, agility and propulsion of the body during locomotion are behaviours with critical importance throughout life, playing a central role in food capture, predator avoidance, reproduction and migration (Schrank and Webb 1998; Drucker and Lauder 2002).

Such fin alterations could be sufficient to affect the population of rostrum dace. Indeed, it is a general assumption in models of host-parasite population dynamics that heavily infested hosts incur higher mortality rates and lower reproductive success than lightly infested or uninfested hosts (Anderson and May 1978). For instance, the copepod *Salmincola* decreases the resistance of its host to environmental stress (Vaughan and Coble 1975; Sutherland and Wittrock 1985) and may decrease the fecundity of female trout (Gall et al. 1972). *Lernaeocera branchialis*, which parasitizes Gadidae living in the Arctoboreal region, has often been associated with host growth reduction (Khan et al. 1993) and mortality (Khan and Lacey 1986; Khan et al. 1990). Heavy *T. polycolpus* infestations may have been an additional stress factor contributing to rostrum dace mortality. It may be necessary to investigate the impact of this ectoparasite on the growth, maturation and physiology of the rostrum dace.

The survival of rostrum dace in France depends on preserving undisturbed rivers with healthy populations. Thus it is essential that most of these rivers and streams are surveyed in the near future. Our results highlight the need to consider parasite communities when preserving stream fish populations.

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References

Anderson RM, Gordon DM (1982) Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. Parasitology 85:373–398

Anderson RM, May RM (1978) Regulation and stability of host-parasite population interactions. I. Regulatory processes. J Anim Ecol 47:219–247

Arkush KD, Giese AR, Mendonca HL, McBride AM, Marty GD, Hedrick PW (2002) Resistance to three pathogens in the endangered winter-run chinook salmon (*Oncorhynchus tshawytscha*): effects of inbreeding and major histocompatibility complex genotypes. Can J Fish Aquat Sci 59:966–975

Arnott SA, Barber I, Huntingford FA (2000) Parasite-associated growth enhancement in a fish-cestode system. Proc R Soc B 267:657–663

Aubrook EW, Fryer G (1965) The parasitic copepod *Tracheliastes polycolpus* Nordmann in some Yorkshire rivers: the first British records. Naturalist Hull 893:51–56

Barber U, Huntingford FA (1995) The effect of *Schistocephalus solidus* (Cestoda: Pseudophyllidea) on the foraging and shoaling behaviour of three-spined sticklebacks, *Gasterosteus aculeatus*. Behaviour 132:1224–1240

Black GA (1982) Gills as an attachment site for *Salmincola edwardsii*. J Parasitol68:1172–1173

Bowen CA, Stedman RM (1990) Host-parasite relationships and geographic distribution of *Salmincola corpulentus* (Copepoda: Lernaeopodidae) on bloater (*Coregonus hoyi*) stocks in Lake Huron. Can J Zool 68:1988–1994

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revised. J Parasitol 83:575–583

Chappaz R, Gilles A, Miquelis A, Cavalli L, Martin JF (1998) Genetic differentiation and hybridization in cyprinid *Leuciscus leuciscus*. C R Acad Sci Paris 321:933–940

Combes C (1995) Interactions durables. Ecologie et évolution du parasitisme. Masson, Paris

Combes C (1996) Parasites, biodiversity and ecosystem stability. Biodivers Conserv 5:953–962

Drucker EG, Lauder GV (2001) Locomotor function of the dorsal fin in teleost fishes: experimental analysis of wake forces in sunfish. J Exp Biol 204:2943–2958

Drucker EG, Lauder GV (2002) Experimental hydrodynamics of fish locomotion: functional insights from wake visualization. Integr Comp Biol 42:243–257

Drucker EG, Lauder GV (2003) Function of pectoral fins in rainbow trout: behavioral repertoire and hydrodynamic forces. J Exp Biol 206:813–826

Fasten N (1921) Studies on parasitic copepods of the genus *Salmincola*. Am Nat 55:449–456

Friend GG (1941) The life-history and ecology of the salmon gill-maggot, *Salmincola salmonea* (L.) (Copepod crustacean). Trans R Soc Edinb 60:503–541

Fryer G (1982) The parasitic copepoda and branchiura of British freshwater fishes. A handbook and key. Freshwater Biological Association, Ambleside

Gall GAE, McClendon EL, Schafer WE (1972) Evidence on the influence of the copepod (*Salmincola californiensis*) on the reproductive performance of a domesticated strain of rainbow trout (*Salmo gairdneri*). Trans Am Fish Soc 101:345–346

Grenfell BT, Dobson AP (1995) Ecology of infectious diseases in natural populations. Cambridge University Press, Cambridge

Gurney R (1933) British freshwater Copepoda, vol 3. Ray Society, London

Hedrick PW, Kim TJ, Parker KM (2001) Parasite resistance and genetic variation in the endangered Gila topminnow. Anim Conserv 4:103–109

Ives AR (1988) Aggregation and the coexistence of competitors. Ann Zool Fenn 25:75–88

Ives AR (1991) Aggregation and coexistence in a carrion fly community. Ecol Monogr 61:75–94

Kabata Z (1986) Redescriptions of and comments on four little-known Lernaeopodidae (Crustacea: Copepoda). Can J Zool 64:1852–1859

Kabata Z, Cousens B (1977) Host-parasite relationships between sockeye salmon, *Oncorhynchus nerka* and *Salmincola californiensis* (Copepoda: Lernaepodidae). J Fish Res Bd Can 34:191–202

Kasahara S (1962) Studies on the biology of the parasitic copepod *Lernaea cyprinacea* Linnaeus and the methods for controlling this parasite in fish-culture ponds. Contrib Fish Lab Fac Agric Univ Tokyo 3:103–196

Khan RA, Lacey D (1986). Effect of concurrent infections of *Lernaeocera branchialis* (Copepoda) and *Trypanosoma murmanensis* (Protozoa) on Atlantic cod, *Gadus morhua*. J Wildl Dis 22:201–208

Khan RA, Lee EM, Barker D (1990) *Lernaeocera branchialis*: a potential pathogen to cod ranching. J Parasitol 76:913–917

Khan RA, Ryan K, Barker DE, Lee EM (1993) Effect of a single *Lernaeocera branchialis* (Copepoda) on growth of Atlantic cod. J Parasitol 79:954–958

Lafferty KD, Morris AK (1996) Altered behaviour of parazitized killifish increases susceptibility to predation by bird final hosts. Ecology 77:1390–1397

Lelek A (1987) Threatened fishes of Europe. Aula, Wiesbaden

Loot G, Lek S, Guégan JF (2001a) Phenotypic modification of roach (*Rutilus rutilus* (L.)) infected with *Ligula intestinalis* (L.) (Cestoda, Pseudophyllidea). J Parasitol 87:1002–1010

Loot G, Brosse S, Lek S, Guégan JF (2001b) Behaviour of roach (*Rutilus rutilus* (L.) altered by *Ligula intestinalis* (L.) (Cestoda: Pseudophyllidea): a field demonstration. Freshw Biol 46:1219–1227

Loot G, Poulin R, Lek S, Guégan JF (2002) The differential effects of *Ligula intestinalis* (L.) plerocercoids on host growth in three natural populations of roach (*Rutilus rutilus* (L.). Ecol Freshw Fish 11:168–177

Lindsey CC (1978) Form, function, and locomotory habits in fish. In: Hoar WS, Randall DJ (eds) Fish physiology: locomotion, vol 7. Academic Press, New York, pp 1–100

Margolis L, Esch GW, Holmes JC, Kuris AM, Shad GA (1982) The use of ecological terms in parasitology. J Parasitol 68:131–133

McGladdery SE, Johnston CE (1988) Egg development and control of the gill parasite, *Salmincola salmoneus*, on Atlantic salmon kelts (*Salmo salar*) exposed to four different regimes of temperature and photoperiod. Aquaculture 68:193–202

Minchella DJ, Scott ME (1991) Parasitism: a cryptic determinant of animal community structure. Trends Ecol Evol 6:250–254

Morand S, Poulin R, Rohde K, Hayward C (1999) Aggregation and species coexistence of ectoparasites of marine fishes. Int J Parasitol 29:663–672

Nagasawa K, Urawa S (2002) Infection of *Salmincola californiensis* (Copepoda: Lernaeopodidae) on juvenile masu salmon (*Oncorhynchus masou*) from a stream in Hokkaido. Bull Natl Salmon Res Center 5:7–12

Norusis MJ (1993) SPSS for Windows. Base system user's guide release 6.0. SPSS, Chicago

Poulin R (1993) The disparity between observed and uniform distributions: a new look at parasite aggregation. Int J Parasitol 23:937–944

Poulin R (1998) Evolutionary ecology of parasites. From individuals to communities. Chapman and Hall, London

Price PW, Westoby M, Rice B (1988) Parasite-mediated competition: some predictions and tests. Am Nat 131:544–555

Sasal P, Niquil N, Bartoli P (2000) Community structure of digenean parasites of sparid and labrid fishesof the Mediterranean sea: a new approach. Parasitology 119:635–648

Schrank AJ, Webb PW (1998) Do body and fin form affect the abilities of fish to stabilize swimming during maneuvers through vertical and horizontal tubes? Environ Biol Fishes 53:365–371

Shaw DJ, Dobson AP (1995) Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. Parasitology 111:S111–S133

Silfverberg H (1999) A provisional list of Finnish Crustacea. Mem Soc Fauna Flora Fenn 75:15–37

Šimková A, Desdevises Y, Gelnar M, Morand S (2000) Co-existence of nine gill ectoparasites (Dactylogyrus: Monogenea) parasitising the roach (*Rutilus rutilus* L.): history and present ecology. Int J Parasitol 10:1077–1088

Šimková A, Gelnar M, Sasal P (2001) Aggregation of congeneric parasites (Monogenea: *Dactylogyrus*) among gill microhabitats within one host species (*Rutilus rutilus* L.). Parasitology 123:599–607

Spillmann CJ (1961) Faune de France, 65 poissons d'eau douce. Lechevalier, Paris

Sutherland DR, Wittrock DD (1985) The effects of *Salmincola californiensis* (Copepoda: Lernaeopodidae) on the gills of farm-raised rainbow trout, *Salmo gairdneri*. Can J Zool 63:2893–2901

Thomas F, Renaud F, Rousset F, Cezilly F, De Meeus T (1995) Differential mortality of two closely related host species induced by one parasite. Proc R Soc LondB 260:349–352

Vaughan GE, Coble DW (1975) Sublethal effects of three ectoparasites on fish. J Fish Biol 7:283–294

Videler JJ (1993) Fish swimming. Fish and fisheries series 10. Chapman and Hall, London

Zar JH (1999) Biostatistical analysis. Prentice Hall, Upper Saddle River