Host specificity of *Argulus coregoni* (Crustacea: Branchiura) increases at maturation

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SUMMARY

We tested the hypothesis that host specificity in ectoparasites does not depend exclusively on the features of the host but also on surrounding habitats, using 2 fish ectoparasites, *Argulus coregoni* and *A. foliaceus* (Crustacea: Branchiura), occurring sympatrically in Finnish lakes. Although these parasites are considered to be of low specificity, we found that the larger of the 2 species, *A. coregoni* developed a pronounced preference for salmonid hosts at the beginning of maturation (defined by the presence of copulating specimens). *Argulus foliaceus* infects a much wider range of fish hosts. We showed that specialization of *A. coregoni* on salmonids does not necessarily result from incompatibility with other fishes, but could instead reflect higher sensitivity of oxygen depletion compared with *A. foliaceus*. Adult *A. coregoni* may meet these demands by attaching to salmonids, the typical inhabitants of well-aerated waters. Young parasites of both species showed little host specificity and attached mainly to fishes with higher body reflectivity. In host choice experiments, *A. coregoni* of 4–5 mm length preferred salmonids (rainbow trout) to cyprinids (roach) irrespective of the type of fish host, on which it had been previously grown in the laboratory. We suggest that such an innate ontogenetic shift in host preference maintains the major part of the parasite population on its principal host, ensuring successful reproduction within suitable habitats.

Key words: fish, parasitic crustaceans, host choice, innate preference, hypoxia.

INTRODUCTION

Host specificity and the factors affecting it are of major interest in ecological parasitology (Poulin, 1998, 2005). The general concepts of principal and auxiliary hosts (Dogiel *et al*. 1961) or required, suitable and unsuitable hosts (Holmes, 1979) are mainly discussed with regard to the suitability of the host's physiology, immunology and ecology to endoparasites (Macinnis, 1976; Poulin, 1992, 1998; Haas, 1994; Sukhdeo and Sukhdeo, 1994). For ectoparasites, we expect that quality of the surrounding habitat is no less important than the suitability of the host body. Some obligate ectoparasites, like crustaceans parasitic on fish, spend a considerable part of their life as free-living animals (Fryer, 1966; Kabata, 1970) i.e. searching for hosts, mating or laying eggs (Mikheev *et al*. 2000; Pasternak *et al*. 2000, 2004).

Some crustacean species ectoparasitic on fish attach to their hosts permanently and lose the ability to move. Others, like some copepods and branchiurans, are not immobile after attachment (Kollatsch, 1959; Stammer, 1959; Kabata, 1970). They are able to change not only their position on the host, but also the host individual. Such changes of individual hosts were recorded, for instance, in obligate ectoparasites of fish, *Argulus* species (Crustacea: Branchiura) (Stammer, 1959; Pasternak *et al*. 2000). These changes may occur only occasionally, due to mechanical disturbance or death of the fish, or they may represent common undisturbed parasite behaviour. It has been shown that both *Argulus foliaceus* and *A. coregoni* can routinely change between individual hosts (Pasternak *et al*. 2000, 2004).

The smaller of the two branchiurans, *A. foliaceus*, lives sympatrically with *A. coregoni* in Finnish lakes. It has a much wider range of potential host species (Herter, 1927; Bower-Shore, 1940; Kollatsch, 1959; Stammer, 1959; Bauer, 1970; Pasternak *et al*. 2000) than *A. coregoni*, which occurs predominantly on salmonid fishes (Shimura, 1983; Valtonen *et al*. 1997; Mikheev *et al*. 2003; Hakalahti and Valtonen, 2003). Our main question is: what limits the distribution of *A. coregoni* among potentially available host species? Is it co-evolution with salmonids or partial segregation between salmonid and non-salmonid fishes within the lakes?

In their early ontogeny, neither *Argulus* species discriminates between different fish species (Pasternak *et al*. 2000; Mikheev *et al*. 2004). They attack and attach to both cyprinids and salmonids,

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preferring fish with higher body reflectivity (Mikheev *et al*. 1998, 2004). *Argulus foliaceus* maintains low host specificity throughout the life-cycle. On the other hand, at the beginning of the reproductive period, *A. coregoni* switches its preference from cyprinids to salmonids (Mikheev *et al*. 2004). We hypothesized (Mikheev *et al*. 2004) that this shift to salmonids occurred because the parasites had been habituated to salmonid fish (rainbow trout *Oncorhynchus mykiss*) from which they were collected for our experiments. In the present study, we aimed to discriminate between acquired and innate preference for salmonids by letting parasites grow on either roach, *Rutilus rutilus*, or rainbow trout before allowing parasites to chose between salmonid and cyprinid fish. If parasites grown on roach later prefer roach to rainbow trout, this would mean an acquired preference; if they prefer rainbow trout, this would imply a genetically programmed preference for salmonids.

If ambient conditions become unfavourable, argulids can leave the habitat together with the fish host or move away on their own. Oxygen deficiency is an important environmental stressor influencing host-parasite interactions (Jokela *et al*. 2005; Saarinen and Taskinen, 2005). Adults of *A. coregoni*, have a body surface to volume ratio about 2 times lower than adults of *A. foliaceus*, so we hypothesize that *A. coregoni* is more sensitive to low oxygen concentration than *A. foliaceus*. In shallow waters with dense vegetation, oxygen deficiency is common during the summer; oxygen saturation can drop almost to zero at night (Hutchinson, 1975; Wetzel, 1983). Salmonid fishes, being strongly restricted to well-oxygenated waters (Wheeler, 1969), avoid such habitats, but many other fishes, especially cyprinids, are common residents there (Varley, 1967).

In the present study we tested the hypothesis that host specificity in argulid crustaceans is related not only to features of the host, but also to features of the habitat. We expect that larger *A. coregoni* are better able to search for, find, and attach to hosts, particularly in running waters with large and fast moving fish. However, the lower surface: volume ratio could make larger parasites more vulnerable to hypoxia and restrict their host range to fish species preferring well-oxygenated waters. More specifically, we tested (1) whether *A. coregoni* is more sensitive to low oxygen than the smaller congeneric, *A. foliaceus*, and (2) whether the preference of *A. coregoni* for salmonids is genetically programmed or results from the host-induced phenotypic plasticity.

MATERIALS AND METHODS

Origin and maintenance of parasites and fish

The experiments were carried out at a commercial fish farm in Central Finland during May and July in 2001 and 2002. To obtain newly hatched metanauplii, stones with overwintered egg clutches of *Argulus coregoni* were collected from a flow-through canal. The stones were placed in shallow white plastic tanks with filtered lake water at 17·8 °C and illumination of 400 lux. Hatching of *A. coregoni* overwintered eggs is mainly triggered by water temperature rising up to 10 °C (Hakalahti and Valtonen, 2003; Mikheev *et al*. 2003). Increased illumination is an additional hatching stimulus (Mikheev *et al*. 2001). The next day, *A. coregoni* started to hatch. Metanauplii were collected with pipettes the day after hatching and kept in filtered water prior to experiments.

Besides metanauplii, 2 groups of older *A. coregoni* were used in experiments on host preference (1) argulids collected from rainbow trout, *Oncorhynchus mykiss* (30–40 cm total length) at the fish farm and (2) argulids reared under controlled laboratory conditions either on rainbow trout or on roach (*Rutilus rutilus*). For the tests on the effect of low oxygen concentration, *A. coregoni* were collected from rainbow trout and *A. foliaceus* from cyprinid and percid fishes caught from the same habitat at the fish farm. Prior to the tests, all parasites were starved for a day to increase feeding motivation (Mikheev *et al*. 2000).

For rearing parasites on 2 types of hosts, rainbow trout of 15–20 cm total length were taken from the rearing ponds of the farm and roach of 14–20 cm total length were caught from an adjacent canal bringing water to the farm. Prior to the experiments, collected fish were thoroughly checked for the presence of ectoparasites, and, if found, they were removed.

Body length of parasites was measured as the distance between the anterior edge of the carapace and the posterior end of the caudal rami. Total length of the fish host was measured.

Testing host preference

To test the host preference of newly hatched (1 day old) and grown up (4–5 mm body length) parasites, groups of 50 juveniles and 20 grown *A. coregoni* were released into 15 litre dark brown, low reflectivity plastic tanks filled with filtered lake water. These tanks provide suitable conditions for host searching, while white or transparent tanks cause aberrant swimming behaviour in argulids (Mikheev *et al*. 1998). Experiments with each size group were replicated 10 times. The illumination was approximately 300 lux and water temperature varied from 15 to 19 °C in accordance with ambient conditions. Fifty newly hatched metanauplii without previous contact with fish were tested for initial host preference. Each test tank contained 2 fish of similar size: 1 rainbow trout (a typical host) and 1 roach (a non-typical host). The number of argulids attached to each host was counted after 15 min of exposure. Individual fish

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were quickly transferred with a hand net into separate white plastic boxes with MS-222 solution. After the hosts were removed from the test tank, the water was checked for unattached parasites. Immobilized fish were thoroughly inspected for the presence of attached parasites. The *A. coregoni* that detached during manipulations were easily recognized against the white background. For each replicate, fresh parasites and fish were used.

To test whether the ontogenetic variation in the host choice of *A. coregoni* is genetically programmed or induced by living on particular fish species initially, we assessed host preference in 2 groups of parasites. One group of *A. coregoni* was reared on a typical salmonid host, *Oncorhynchus mykiss*, another on a cyprinid fish, *Rutilus rutilus*. The rearing procedure, growth and development of parasites have been described previously (Pasternak *et al.* 2004). Parasite preference for either 1 specimen of *O. mykiss* or 1 *R. rutilus* simultaneously presented was tested as described above. The tests were run twice, using parasites after 15 h or 3 weeks of attachment on their hosts. By that time, parasites reached mean body length of 4–5 mm (Pasternak *et al.* 2004). In the first test, 50 metanauplii were released into a tank with 2 hosts (1 rainbow trout and 1 roach), and in the second test, 20 larger parasites were used per tank.

Testing sensitivity to low oxygen

To test the hypothesis that *A. coregoni* is more sensitive to low oxygen concentration than *A. foliaceus*, we mimicked the conditions of a shallow water habitat with dense bottom vegetation. Forty plastic boxes of 2 l each were filled with lake water (the range of oxygen concentration was 7·2–9·1 mg l^{-1}) and the macrophytes *Myriophyllum* and *Elodea*. They were tightly covered with lids and placed in a dark room for 4 h to reduce oxygen levels. After 4 h, a perforated plastic cylinder was introduced into the centre of each box, oxygen concentration was measured (it varied from 0·11 to 0·58 mg l^{-1} between the boxes), and 10 free-swimming parasites were released into the cylinder. Ten replicates were conducted with both adult males and females of *A. coregoni*, as well as with both sexes of *A. foliaceus*. Small holes in the bottom and walls of the cylinders allowed water to penetrate inside, but kept parasites confined and observable. The boxes again were covered with lids and placed in the dark for 1 more hour. After that, oxygen concentration was measured within each cylinder and the numbers of either free-swimming or immobile parasites were counted. By the end of the exposure, oxygen concentration was within the range 0·5 to 0·81 mg l^{-1}. The immobile parasites from each box were transferred into forty 1 litre boxes filled with aerated (85–105% oxygen saturation) water, and after 1 h, the numbers of free-swimming and immobile individuals were counted.

Occurrence of A. foliaceus *and* A. coregoni *on rainbow trout in stagnant and running waters*

To check whether the occurrence of *A. coregoni* on rainbow trout was higher in running waters than that of *A. foliaceus*, 10 fish were randomly collected from 2 habitats within the same fish farm. One habitat was a canal with water flow at the surface of 0·3–1·1 m/s; the second habitat was several flow-through ponds with current velocity less than 0·1 m/s. The number of parasites of both species was counted from individual fish. Mean body length of fish from the pond (34·5 ± 5·8 cm, mean ± S.D.) and the canal (37·0 ± 6·3 cm) (*t*-test: $P = 0{\cdot}517$) did not differ.

Host searching efficiency in the dark and light

Searching for and attaching to fish hosts is likely more strenuous in flowing waters. *Argulus coregoni* inhabiting running and turbulent waters are likely to rely more on visual than on olfactory or hydromechanical cues (Mikheev *et al.* 2004). The relative importance of vision could be indirectly assessed by comparing infection rates in dark versus light, conditions, all else being equal.

To compare the searching ability of *A. coregoni* and *A. foliaceus*, test groups of 10 adult parasites were released into 15 litre dark brown, low reflectivity plastic tanks filled with filtered lake water. In pilot experiments, no differences in host searching and attachment rate between males and females of either *Argulus* species were found, so 10 specimens from a random mixture of both sexes were included in each replicate. The illumination in the light treatment was about 300 lux and the water temperature was 20 °C. The water temperature was the same in the dark tests. Each test tank contained 1 brown trout, *Salmo trutta*, of 21 ± 2·3 mm fork length. The number of argulids attached to the host was counted after 15 min of exposure. After exposure fish were quickly transferred with a hand net into a white plastic box with MS-222 solution. Immobilized fish were thoroughly inspected for the presence of attached parasites. After the hosts were removed from the tank, the water was checked for unattached parasites. Twelve replicates for each parasite species were carried out in both dark and light conditions. New animals, both parasites and fish, were used in each replicate.

Data analysis

The effects of *A. coregoni* acclimation to different fish hosts (rearing of parasites either on roach or on rainbow trout) and type of available fish (roach *vs* rainbow trout) on intensity of infection in the cross-infection experiment were tested by two-way ANOVA, and differences between groups were analysed with post-hoc Tukey's honestly significant

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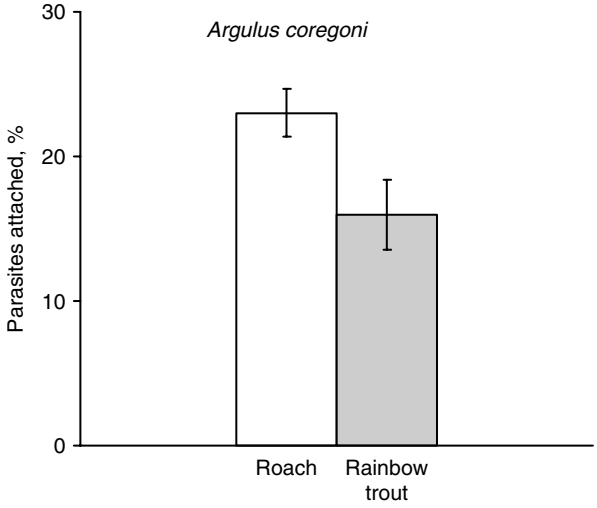


Fig. 1. Host preference in newly hatched metanauplii of *Argulus coregoni* that had no previous contact with any fish. Fifty *A. coregoni* were released into a tank with 1 rainbow trout and 1 roach of similar size. White columns: percentage of parasites attached to roach; grey columns: to rainbow trout. S.E. bars are given.

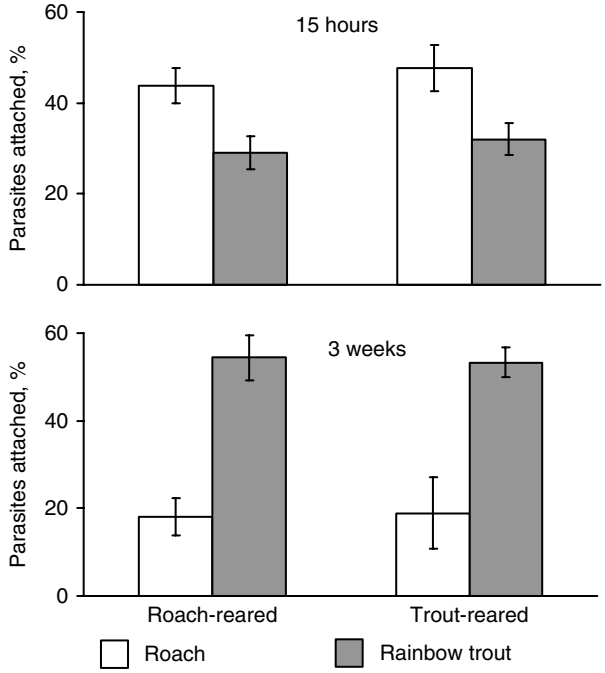


Fig. 2. Host preference in 'cross infection' experiments with *Argulus coregoni*. Upper panel: newly hatched parasites tested after being attached to fish for 15 h, either roach (left group of bars), or rainbow trout (right group of bars). Lower panel: parasites tested after 3 weeks rearing either on roach (left group of bars), or rainbow trout (right group of bars). White columns: percentage of parasites attached to roach; grey columns: to rainbow trout. S.E. bars are shown.

difference (HSD) tests. The same tests were used to analyse the resistance of adult parasites to low oxygen concentration using species (*A. coregoni*, *A. foliaceus*) and sex (males, females) as factors. Two-way ANOVAs were also used to compare the abundance of *A. coregoni* and *A. foliaceus* on salmonids in running and stagnant waters as well as to compare host attachment rates in light and dark treatments. Data were $\log_{10}(x+1)$ transformed to satisfy ANOVA assumptions. Data for all experiments were checked for normality and homogeneity of variance. Differences in intensity of infection of newly hatched metanauplii *A. coregoni* on 2 alternative fish hosts were assessed with Mann-Whitney U-test.

RESULTS

Host preference in newly hatched parasites

Newly hatched metanauplii of *A. coregoni* which had no previous contact with any fish preferred roach to rainbow trout when given a choice between these hosts (Fig. 1) (Mann-Whitney U test: $Z=-2{\cdot}6451$, $P=0{\cdot}0082$).

Host preference of A. coregoni *reared on different fishes*

Contact with either cyprinid (roach) or salmonid (rainbow trout) hosts for 15 h did not change the patterns of *A. coregoni* host preference (Fig. 2). Argulids preferred roach to rainbow trout regardless of the host they were initially attached to (two-way ANOVA: acclimated to roach *vs* acclimated to trout, $F_{1\cdot36}$, $P=0{\cdot}2565$; preference for roach *vs* trout, $F_{1\cdot36}$, $P=0{\cdot}0002$) (Tukey's HSD: preference for roach against trout among parasites acclimated to trout, $P=0{\cdot}0291$; preference for roach against trout among parasites acclimated to roach, $P=0{\cdot}0222$). No interaction between acclimation and preference for alternative hosts was observed (two-way ANOVA: $F_{1\cdot36}$, $P=0{\cdot}9379$). The next test was done when *A. coregoni* reached 3 weeks age, and the first copulating pairs were observed. In our previous experiments at 18–20 °C, *A. coregoni* adults laid their first egg clutches at the age of 5 weeks (Pasternak *et al.* 2004). Regardless of the host they were reared on 3-week-old parasites demonstrated a pronounced preference for the salmonid *O. mykiss*, provided equal availability of both salmonid and cyprinid hosts (Fig. 2) (two-way ANOVA: reared on roach *vs* reared on trout, $F_{1\cdot36}$, $P=0{\cdot}8783$; preference for trout *vs* roach, $F_{1\cdot36}$, $P<0{\cdot}0001$) (Tukey HSD: preference for trout against roach among parasites acclimated to trout, $P=0{\cdot}0002$; preference for trout against roach among parasites acclimated to roach, $P=0{\cdot}0002$). No interaction between the factors was observed (two-way ANOVA: $F_{1\cdot36}$, $P=0{\cdot}8575$).

Sensitivity to hypoxia in A. coregoni *and* A. foliaceus

Adults of *A. coregoni* were much less resistant to low oxygen concentration than *A. foliaceus*. After 1 h at

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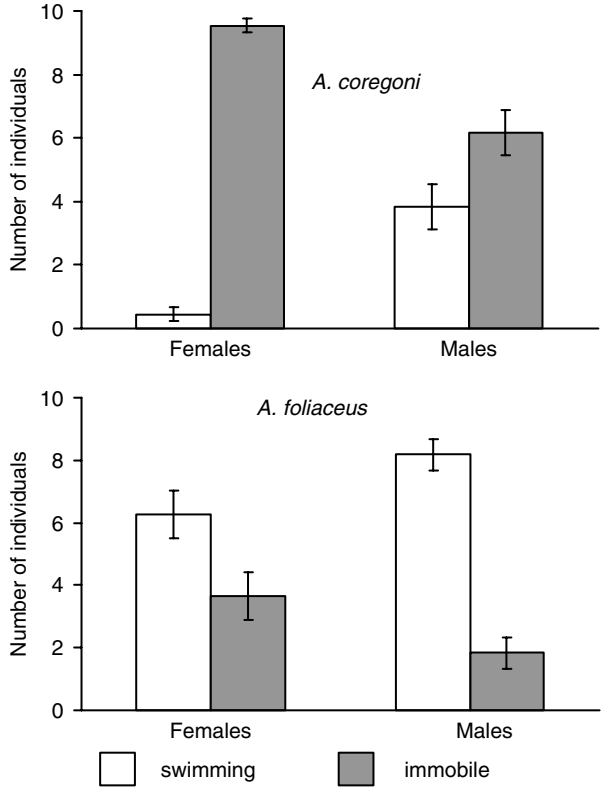


Fig. 3. Effect of low oxygen concentration on *Argulus coregoni* (upper panel) and *Argulus foliaceus* (lower panel) behaviour. White columns: number of swimming parasites; grey columns: number of immobile parasites after 1 h of exposure to 2–7% oxygen saturation. S.E. bars are shown.

an oxygen saturation of less than 10%, most *A. coregoni* were lying immobile on the bottom of the cylinder (Fig. 3), while most *A. foliaceus* continued swimming ($F_{1,36}=119{\cdot}8$, $P<0{\cdot}0001$). Females were more sensitive to oxygen deprivation than males (Fig. 3) ($F_{1,36}=43{\cdot}8$, $P<0{\cdot}0001$). However, a significant difference between the sexes was observed only in *A. coregoni* (Tukey HSD, *A. coregoni*: $P=0{\cdot}0002$; *A. foliaceus*: $P=0{\cdot}3675$). All the immobile *A. foliaceus* transferred into well-oxygenated water resumed normal swimming after 1 h, but none of the *A. coregoni* started to move.

Occurrence of A. foliaceus *and* A. coregoni *on salmonid fishes in stagnant and running waters*

Rainbow trout from the canal had higher infection intensities than those from the pond (two-way ANOVA: $F_{1,36}=15{\cdot}64$, $P=0{\cdot}0003$). *Argulus coregoni* was significantly more abundant on *O. mykiss* than *A. foliaceus* (two-way ANOVA: $F_{1,36}=27{\cdot}35$, $P<0{\cdot}0001$). A significant interaction was observed ($F_{1,36}=38{\cdot}25$, $P<0{\cdot}0001$): in the pond, fish were equally infected with both parasite species (Tukey HSD: $P=0{\cdot}905$), but in the canal, *A. coregoni* was much more abundant than *A. foliaceus* (Tukey HSD: $P=0{\cdot}0002$).

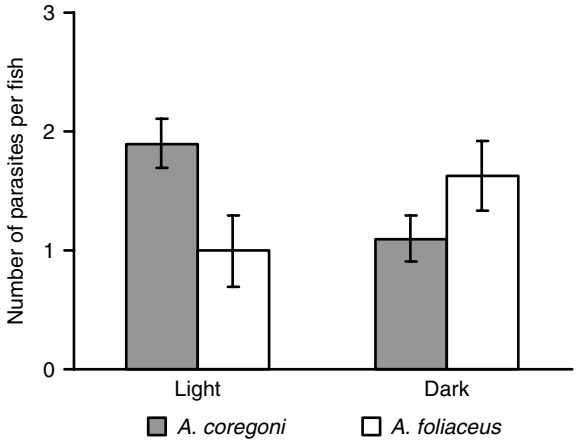


Fig. 4. Host searching success of *Argulus coregoni* and *Argulus foliaceus* in the dark and light as the number of parasites attached to the host during 15 min exposure. Grey columns – *A. coregoni*, white columns – *A. foliaceus*. S.E. bars are shown.

Attachment to hosts in the dark and light

There were no differences in the host attachment rate between the 2 tested parasite species (two-way ANOVA: $F_{1,44}=0{\cdot}093$, $P=0{\cdot}7616$), or between light and dark conditions ($F_{1,44}=0{\cdot}0020$, $P=0{\cdot}9649$). However, a significant interaction between factors was observed ($F_{1,44}=11{\cdot}316$, $P=0{\cdot}0011$; Fig. 4). Post-hoc comparison revealed that *A. coregoni* had a higher rate of attachment in the light (Tukey HSD: $P=0{\cdot}0101$), whereas *A. foliaceus* had a higher attachment rate in the dark (Tukey HSD: $P=0{\cdot}0408$).

DISCUSSION

Our results suggest that habitat features could play a noticeable role in shaping the host specificity of argulid ectoparasites by restricting the range of suitable fishes. *Argulus coregoni* can spend its entire life on a single host individual (Pasternak *et al*. 2004), and young stages can infect a wide range of fish species (Mikheev *et al*. 2004). However, low specificity only seems typical of young *A. coregoni*. At maturation, there is a clear preference for salmonid fishes. Our results support the hypothesis that high sensitivity to oxygen content, not specific characteristics of the host itself, favours parasites that infect fish from well-oxygenated waters, making salmonids suitable hosts. Choosing a 'wrong' host, e.g. a cyprinid, does not mean inevitable death of the parasites, but a reduction in fitness is highly probable. Such a host could take egg-carrying females to stagnant oxygen-deficient habitats, which lack suitable substrata for egg laying. Eggs of *A. coregoni* are laid on hard substrata, preferably stones (Shimura, 1983; Mikheev *et al*. 2001; Hakalahti *et al*. 2004), which are rare in typical cyprinid habitats (Varley, 1967).

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The cross-infections, however, clearly showed that *A. coregoni* preference for salmonids is innate, and not acquired through habituation to the hosts chosen by newly hatched larvae. Host specificity is low in small metanauplii beginning to look for a host, but host preferences become clear in adult parasites when marked signs of sexual maturation are evident (Pasternak *et al*. 2004; Mikheev *et al*. 2004). *Argulus coregoni* of 4–5 mm in length collected from farmed *O. mykiss* demonstrate a pronounced preference for salmonid fishes (Mikheev *et al*. 2004). In the early ontogeny of this obligate parasite, the crucial problem for small and fast growing *A. coregoni* (Pasternak *et al*. 2004) with high-energy demands (Mikheev *et al*. 2000) is to locate and attach to a fish host. Early specialization on salmonids would prolong the hard and energy-consuming task of host searching. Newly hatched free-swimming metanauplii can only survive without a host for 2–5 days (Kollatsch, 1959; Pasternak *et al*. 2000; Hakalahti *et al*. 2005), and, therefore, they cannot be very choosy. By 7–10 days after hatching, free-swimming parasites rely predominantly on visual cues for host finding, preferring fish with higher body reflectivity (Mikheev *et al*. 2004). Young *A. coregoni*, with body length less than 2 mm, readily concentrate over a white disc placed against a dark background; the addition of fish-conditioned water does not influence this behaviour. For larger individuals, trout-conditioned water significantly enhanced this behaviour, but roach-conditioned water had no effect (Mikheev *et al*. 2004). The response to host chemical cues was observed at the same developmental stage in which the change of preference from roach towards trout occur (Mikheev *et al*. 2004). Despite the initial lack of preference for salmonids, this preference develops later in *A. coregoni* ontogeny, regardless of the initially chosen host. This supports the hypothesis that the observed ontogenetic shift in *A. coregoni* host preference towards salmonid fishes is genetically programmed. No pronounced ontogenetic changes in host preference have been observed for *A. foliaceus* (Mikheev *et al*. 1998, 2000; Pasternak *et al*. 2000).

The ontogenetic changes in *A. coregoni* behaviour reflect the shifting challenges faced during parasite development. After hatching, the main task for small, free-swimming *A. coregoni* is to find a source of food, i.e. a suitable fish host, as soon as possible. Low oxygen content is not so dangerous for young parasites (our unpublished data). As parasites grow, their surface area to body volume ratio decreases, perhaps making respiration more difficult. Sensitivity to oxygen concentration may then become an important factor restricting host preference. The larger size and higher sensitivity to low oxygen of *A. coregoni*, compared to *A. foliaceus*, may prevent establishment of the former species into littoral habitats with dense vegetation. On the other hand, the large size of *A. coregoni* could be beneficial for finding and attaching to large hosts with low population density. This may be the case in rivers and streams, where running, turbulent water deters the use of hydromechanical and chemical stimuli to locate potential hosts (Moore *et al*. 1994; Bouwma and Hazlett, 2001; Webster and Weissburg, 2001). Vision seems more useful in moving water. Indeed, *A. coregoni* had a higher infection rate in light conditions. Its smaller congeneric, *A. foliaceus*, was more efficient in the dark, probably because it efficiently uses its olfaction and hydromechanical sense (Mikheev *et al*. 2000). These cues are probably more useful in stagnant waters with relatively high fish population densities. The population density of the two parasites differed between a flow-through canal and pond, as we expected on the basis of the parasites different host finding strategies.

Reproductive value is low for young individuals that have only a low probability of surviving to reproductive maturity, but it increases steadily towards the period of reproduction (Charlesworth, 1980). The closer *A. coregoni* is to egg laying, the more restricted parasites are in their host choice, because failure at this stage is most costly. For adults of *A. coregoni*, especially for gravid females, it is crucial to be in well-oxygenated habitats with stones suitable for egg laying.

Genetically programmed ontogenetic changes in behaviour and host preference are not exclusive to parasites with complex life-cycles, like many helminths (Price, 1980; Begon *et al*. 1990). We found that a genetically programmed change in *A. coregoni* host preference can persist regardless of the first host used by a parasite. Specific habitat requirements of mature *A. coregoni* bind them with salmonid fishes and likely favour host switching of larger parasites if they initially infect a non-salmonid. The ability of branchiuran ectoparasites to leave the host and locate to another one (Pasternak *et al*. 2000, 2004) provides flexibility in host and habitat choices. The somewhat lower growth and development of *A. coregoni* on non-salmonid hosts (Pasternak *et al*. 2004) could be related to a lower residence time on cyprinids than on salmonids.

Despite the marked ontogenetic shift in host preference, *A. coregoni* retains an ability to attach and survive on hosts other than salmonids. Although fitness on such 'supplementary' hosts is expected to be lower (Pasternak *et al*. 2004), these hosts could maintain the parasite population in case of a sudden drop in salmonid populations.

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