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Parasite loads on fish have been shown to be influenced by the size of the host (Kabata, 1981; Grutter, 1994). The general trend is that a larger host will harbour higher numbers of ectoparasites (Tucker et al., 2002). The reasons for this may be partly related to the hosts age (larger hosts are generally older) with older hosts having had longer to accumulate parasites, and partly related to the surface area of the host as a larger host has a larger surface area making it easier for parasites to locate and attach to them (Kuris et al., 1980, and references therein). This trend has not been tested for branchiuran ectoparasites before.

Crustacean ectoparasites on fish provide an excellent model for studying parasite distribution within a host population due to the relative ease in identifying and counting them. Parasites from the genus *Argulus* are regarded as the most widespread and problematic parasites in freshwater fish culture (Kearn, 2004; Walker et al., 2004). These parasites have been responsible for significant economic losses in aquaculture (Menezes et al., 1990) and recreational fishery operations (Taylor et al., 2006). Despite this, there are still huge gaps in our understanding of the way in which these parasites interact with their hosts.

*Argulus foliaceus* (L., 1758), is regarded as non-host-specific and has been recorded from practically every freshwater fish species within its natural range (Stammer, 1959; Kennedy, 1974). Despite the opportunistic nature of this parasite some hosts still appear to be more susceptible than others (Bandilla et al., 2005). The factors influencing the distribution of *A. foliaceus* within a host population,
however, are still poorly studied. In this investigation we analysed a stickleback population from a recreational fishing lake in the south-west of England.

Three-spined sticklebacks, *Gasterosteus aculeatus* (L., 1758) are commonly found in temperate waterbodies of the northern hemisphere (Wootton, 1976). Because of their role in the food web as both predators and prey they are consequently hosts in many parasite life cycles (Kalbe et al., 2002). As a result, they may also serve as reservoirs for some parasite species, transmitting parasites to other fish residing in the same habitats. Three-spined sticklebacks breed in the warm shallow regions of ponds and lakes (Davies et al., 2004), which are the same regions preferred for egg deposition by *A. foliaceus*. This will expose sticklebacks to this parasite throughout the breeding season and as such one would expect a high infection intensity and prevalence on this fish species. The authors have previously found one adult male three-spined stickleback with 143 larval *A. foliaceus* attached to it (P. D. Walker, unpubl.). However, juvenile sticklebacks appear to show behavioural changes including an increase in shoaling behaviour in the presence of argulid lice (Poulin, 1999). These changes in behaviour probably reduce the risk of individuals being parasitized.

Three-spined sticklebacks were caught from the littoral regions of the lake using a standard pond net. Upon capture, the standard length of each fish was recorded and the number of attached parasites noted. Statistical analyses were carried out using Quantitative Parasitology 3.0 (QP 3.0: Reiczigel & Rózsa, 2005) and INSTAT.

Fifty-three sticklebacks were caught varying in length from 13 to 44 mm. Sixteen of the fish were $\leq$ 20 mm long, only 1 fish was found between 21 and 30 mm long, and the remaining 36 fish were $>31$ mm long. Thirty of the fish were infected with *A. foliaceus*, giving a parasite prevalence of 56% (95% confidence limits: 42 to 70%). The mean infection intensity was 7.33 (95% confidence limits: 5.43 to 9.57; $n = 30$) and the maximum number of lice recorded on an individual fish was 23. The average length of infected sticklebacks was significantly greater (Mann-Whitney U-test, 2-tailed $P$-value < 0.0001) than that of the uninfected sticklebacks (fig. 1). In addition, all infected fish were found to be more than 30 mm in length (fig. 2).

The size distribution of the sticklebacks probably reflects two distinct year classes. For many parasite species the infection intensity is often related to the size of the host, with larger hosts generally being older and therefore having had longer to accumulate parasites (Kuris et al., 1980). However, this trend probably does not apply for intermittent parasites such as *Argulus* species as these parasites frequently leave their hosts throughout their lives. Therefore, the greater number of parasites found on the larger hosts must be attributable to some other factor.
Fig. 1. Mean standard length of *Argulus foliaceus* (L., 1758) infected (n = 30), and uninfected three-spined sticklebacks, *Gasterosteus aculeatus* (L., 1758) (n = 23). Error bars = ±1 s.d.

Juvenile sticklebacks can and do exhibit parasite avoidance behaviour (Poulin & FitzGerald, 1988; Dugatkin et al., 1994). Mikheev et al. (2003), observed a similar behavioural trait in juvenile roach, *Rutilus rutilus* (L., 1758). It is plausible that the lack of parasites on small sticklebacks in this study is a result of parasite avoidance behaviour. It is also plausible that below a certain size threshold *Argulus* simply does not regard fish as a host and that *A. foliaceus* is in fact size-selective when locating a suitable host. Poulin & FitzGerald (1988) proposed that it may be adaptive for *Argulus funduli* Krøyer, 1863 (incorrectly identified as *A. canadensis* Wilson, 1916; see Poulin, 1999) to parasitize smaller hosts as larger fish capture
and eat more parasites. However, our data for A. foliaceus and three-spined sticklebacks do not appear to support this hypothesis.

In conclusion, our study demonstrates a possible size-based difference in susceptibility amongst three-spined sticklebacks. We hypothesize that this susceptibility is caused by behavioural interplays between the sticklebacks and A. foliaceus, although parasite-induced mortality of very small fish cannot be ruled out. Future studies involving the interactions between Argulus foliaceus and three-spined sticklebacks are required to fully elucidate the reasons for our observations.

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LITERATURE CITED


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