Growth and energetics in the stickleback–*Schistocephalus* host–parasite system:
a review of experimental infection studies

Iain Barber\(^1,4\), Hazel A. Wright\(^2\), Stephen A. Arnott\(^3\) &
Robert J. Wootton\(^2\)

\(^1\) Department of Biology, Adrian Building, University of Leicester, Leicester LE1 7RH, UK;
\(^2\) Institute of Biological Sciences, University of Wales Aberystwyth, Aberystwyth, UK;
\(^3\) School of Biological Sciences, University of Aberdeen, Aberdeen, UK

(Accepted: 18 December 2007)

Summary

Three-spined sticklebacks in natural lacustrine populations are often infected with plerocercoids of the indirectly transmitted pseudophyllidean cestode *Schistocephalus solidus*. Field studies typically show infections to be associated with reduced host condition, gonadogenesis and energy reserves, though infection phenotypes can vary considerably both between and within host populations. Experimental infection studies allow the impact of infections on hosts to be studied under a variety of rearing conditions, and so can be used to determine the environmental component of infection phenotypes. Here, we review recent laboratory studies undertaken by our group, examining the growth and condition of experimentally infected fish reared under conditions that differed in terms of absolute ration, temporal pattern of feeding and level of competition between fish. We compare infection phenotypes generated in our experimental studies with those of fish sampled in field based studies. Experimental studies in which infected fish were reared under competition for limited food resources, or were fed a restricted diet, generated infection phenotypes that most closely resembled those found in the majority of natural populations. When access to food was unrestricted, however, infected fish were able to sustain high growth rates and lay down energy reserves. If experimental studies are to be used to understand the impact of infection under natural conditions, husbandry protocols that closely match field conditions must be designed. We suggest that a full understanding of the impact of parasites on their hosts can only be gained by integrating controlled laboratory experiments with detailed field studies. The stickleback–*Schistocephalus* system is ideally suited to examining these questions, and we provide several suggestions for future research.

---

\(^4\) Corresponding author’s e-mail address: ib50@le.ac.uk

© Koninklijke Brill NV, Leiden, 2008

Behaviour 145, 647-668

Also available online - www.brill.nl/beh
Introduction

*Schistocephalus solidus* (Cestoda: Pseudophyllidea) is a common, widespread, macrohelminth parasite of three-spined sticklebacks *Gasterosteus aculeatus* in lacustrine and some slow flowing, freshwater habitats, throughout the distribution of the fish (Kennedy, 1974; Wootton, 1976, 1984; Barber, 2007). Sticklebacks acquire the infection when they ingest infective procercoids present in the haemocoel of infected copepods. After being consumed by sticklebacks the procercoids penetrate the intestine wall and develop into plerocercoids in the fish’s body cavity (see Figure 1). The parasite attains sexual maturity in the intestine of a piscivorous endotherm (typically a bird) following predation of the host fish. Eggs pass out from the bird into the aquatic environment then hatch into free swimming coracidia, which are ingested by feeding copepods (Smyth, 1994). The life cycle is, therefore, indirect, since it includes three different host taxa, and transmission between these hosts is via the food web, i.e., it is a trophically transmitted parasite. Infected sticklebacks exhibit altered behaviours, including impaired escape responses following simulated avian attacks (Giles, 1983; Barber et al.,

![Figure 1](image_url)

**Figure 1.** Photographs showing a three-spined stickleback infected with the cestode *Schistocephalus solidus*. Panel (b) shows an infected fish following a clearing and staining procedure, which makes the fish flesh translucent and allows the lozenge-shaped plerocercoid (p) to be seen inside the body cavity.