



An experimental approach to the immuno-modulatory basis of host-parasite local adaptation in tapeworm-infected sticklebacks



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HIGHLIGHTS

- Icelandic sticklebacks more resistant to *S. solidus* than DE and ES origins.
- *S. solidus* from Iceland were more virulent as DE and ES origins.
- Host exploitation was almost identical across sympatric host-parasite combinations.
- Stickleback origins differed in *in vitro* leukocyte activity.
- *S. solidus* secretory excretory products showed only little local adaptation.

GRAPHICAL ABSTRACT



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ABSTRACT

The evolutionary arms race of hosts and parasites often results in adaptations, which may differ between populations. Investigation of such local adaptation becomes increasingly important to understand dynamics of host-parasite interactions and co-evolution. To this end we performed an infection experiment involving pairs of three-spined sticklebacks and their tapeworm parasite *Schistocephalus solidus* from three geographically separated origins (Germany, Spain and Iceland) in a fully-crossed design for sympatric and allopatric host/parasite combinations. We hypothesized that local adaptation of the hosts results in differences in parasite resistance with variation in parasite infection rates and leukocyte activation, whereas parasites from different origins might differ in virulence reflected in host exploitation rates (parasite indices) and *S. solidus* excretory-secretory products (SsESP) involved in immune manipulation.

In our experimental infections, sticklebacks from Iceland were more resistant to *S. solidus* infection compared to Spanish and German sticklebacks. Higher resistance of Icelandic sticklebacks seemed to depend on adaptive immunity, whereas sticklebacks of German origin, which were more heavily afflicted by *S. solidus*, showed elevated activity of innate immune traits. German *S. solidus* were less successful in infecting and exploiting allopatric hosts compared to their Icelandic and Spanish conspecifics. Nevertheless, exclusively SsESP from German *S. solidus* triggered significant *in vitro* responses of leukocytes from naïve sticklebacks. Interestingly, parasite indices were almost identical across the sympatric combinations.

Differences in host resistance and parasite virulence between the origins were most evident in allopatric combinations and were consistent within origin; i.e. Icelandic sticklebacks were more resistant and their *S. solidus* were more virulent in all allopatric combinations, whereas German sticklebacks were less resistant and their parasites less virulent. Despite such differences between origins, the degree of

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host exploitation was almost identical in the sympatric host–parasite combinations, suggesting that the local evolutionary arms race of hosts and parasites resulted in an optimal virulence, maximising parasite fitness while avoiding host overexploitation.

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1. Introduction

Local adaptation has been described for a number of host–parasite systems (Lively and Jokela, 1996; Kaltz and Shykoff, 1998; Imhoof and Schmid-Hempel, 1998; Gandon, 1998; Lajeunesse and Forbes, 2002; King et al., 2011; Lagrue et al., 2016) and becomes increasingly important in investigations on host parasite co-evolutionary dynamics (Kawecki and Ebert, 2004; Ebert, 2008; Lion and Gandon, 2015; Auld and Tinsley, 2015). The paradigm that host dispersal is the driver of parasite genetic structures has been challenged and it has been proposed that other factors are important for local adaptation in host–parasite systems (Maze-Guilmo et al., 2016). Current research in this field asks for approaches in which observations in the wild can be combined with the experimental testing of hypotheses in laboratories (Kawecki and Ebert, 2004; Blanquart et al., 2013; Maze-Guilmo et al., 2016). Here, we compared three host–parasite pairs of three-spined stickleback (*Gasterosteus aculeatus*) and their cestode *Schistocephalus solidus*, which differ in parasite abundance in their natural habitats, in a controlled laboratory infection experiment.

The three-spined stickleback is a well-suited model organism to study local host–parasite adaptations (Eizaguirre et al., 2012; Konijnendijk et al., 2013; Lenz et al., 2013b; Stutz et al., 2015), reviewed in (Barber, 2013; Scharsack et al., 2016). Sticklebacks are widely distributed across marine and freshwater habitats in which they are exposed to a variety of parasite species (Kalbe et al., 2002; Barber, 2007; MacColl, 2009; Eizaguirre et al., 2011; de Roij and MacColl, 2012; Feulner et al., 2013; Stutz et al., 2014; Karvonen et al., 2015).

It has been illustrated that stickleback hosts differ in their immunocompetence across origins, presumably depending on the local parasite infection pressure (Wegner et al., 2003; Kalbe and Kurtz, 2006; Scharsack et al., 2007a; Eizaguirre et al., 2011; Eizaguirre et al., 2012; Lenz et al., 2013a; Scharsack and Kalbe, 2014). However, yet little information is available on whether the parasites adapt their virulence to their local hosts too, but see (Kalbe et al., 2016).

With their often complex life cycles helminth parasite species, such as the cestode *Schistocephalus solidus*, are particularly suited to such studies due to their longevity, which can involve long-term contact with the immune systems of their vertebrate hosts (Barber, 2013). *S. solidus* infects cyclopoid copepods as first (Hafer and Milinski, 2016), three-spined sticklebacks as obligatory and specific second (Bråten, 1966; Orr et al., 1969) and most often fish-eating birds as final hosts, in which it reproduces either by selfing or outcrossing (Christen et al., 2002; Milinski, 2006). *S. solidus* spends most of its lifetime in the body cavity of its stickleback host, where it gains most of its weight and reproductive capacity (Milinski, 2004), reviewed in (Hammerschmidt and Kurtz, 2009; Barber and Scharsack, 2010).

To increase the likelihood of predation by the final host, *S. solidus* manipulates the anti-predator, shoaling and foraging behaviour of its stickleback host (Milinski, 1984, 1985; Godin and Sproull, 1988; Barber and Huntingford, 1995). To facilitate

exploitation of its stickleback host, the activity of the stickleback's immune system is manipulated by the parasite, resulting in reduced responsiveness of granulocytes to parasite antigens *in vitro* (Scharsack et al., 2004) and fluctuating kinetics of lymphocyte and monocyte proliferation *in vivo* (Scharsack et al., 2007b). However, sticklebacks endowed with optimal numbers of MHC alleles are able to constrain the growth of the parasite more efficiently than those with suboptimal numbers of MHC alleles (Kurtz et al., 2006).

Given the fatal behavioural manipulation of the stickleback, selective pressure on the host is likely to be strong to avoid infection with *S. solidus*. Its host-specificity (Bråten, 1966; Orr et al., 1969; Henrich et al., 2013) and enormous growth in the intermediate host (Orr and Hopkins, 1969), both indicate strong genotype–genotype (GxG) interactions. This makes it an excellent system to study host–parasite fitness trade-offs and effects of environmental variation on host parasite interactions (GxGxE) and potential local adaptation.

Indirect evidence for local adaptation of *S. solidus* comes from *in vitro* studies. After analysis of *S. solidus* excretory-secretory products (SsESP) for their capacity to modulate stickleback leukocyte responses *in vitro*, it was suggested that the intensity of immune manipulation was dependent on parasite origin (Scharsack et al., 2013). Using antigen preparations from *S. solidus*, it was observed that the magnitude of the *in vitro* leukocyte response depended on the origin of the parasite (Franke et al., 2014). Interestingly, higher leukocyte responses were observed with antigens from populations with high (20–50%) *S. solidus* prevalence (Franke et al., 2014).

More direct evidence for local adaptation of *S. solidus* comes from a fully-crossed infection experiment. Kalbe et al. (2016) compared two stickleback populations naturally infected with *S. solidus*, one of which with high (>20%) *S. solidus* prevalence from Lake Skokseidsvadnet in Norway and the other with low (<1%) *S. solidus* prevalence from a brackish lagoon of the Baltic Sea. The allopatric infection combinations suggested that Norwegian sticklebacks were more resistant than German ones and that Norwegian *S. solidus* were more virulent than their conspecifics from the German population. Interestingly, both parasites grew equally well in their sympatric hosts, suggesting that the locally ongoing evolutionary arms race resulted in an optimal virulence of the parasite.

With the present study, we expected to find higher levels of host resistance and parasite virulence in sticklebacks and *S. solidus* originating from populations with high levels of *S. solidus* prevalence.

In the present study, three host parasite origins with increasing prevalence of *S. solidus*, ranging from 3 to 5% in a German (DE) (Franke et al., 2014), over 7–15% in an Icelandic (IS) (Karvonen et al., 2013) to 40–66% in a Spanish (ES) origin (Prieto et al., 2005) were used. Using these origins, we designed an infection experiment involving laboratory F1 offspring of sticklebacks and *S. solidus* in a fully-crossed design for sympatric and allopatric combinations. We analysed the infection success of the parasite and the activity of stickleback head kidney leukocytes (HKL) (subsequently referred to

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