International Journal for Parasitology xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

International Journal for Parasitology

journal homepage: www.elsevier.com/locate/ijpara

Accumulation and exchange of parasites during adaptive radiation in an ancient lake ☆

Joseph E. Ironside *, Toby J. Wilkinson

Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth, Ceredigion SY23 3DA, United Kingdom

ARTICLE INFO

Article history:
Received 6 July 2017
Received in revised form 11 October 2017
Accepted 21 October 2017
Available online xxxx

Keywords:
Lake Baikal
Amphipod
Microsporidia
Adaptive radiation
Parasite

ABSTRACT

In the ancient Lake Baikal, Russia, amphipod crustaceans have undergone a spectacular adaptive radiation, resulting in a diverse community of species. A survey of microsporidian parasites inhabiting endemic and non-endemic amphipod host species at the margins of Lake Baikal indicates that the endemic amphipods harbour many microsporidian parasite groups associated with amphipods elsewhere in Eurasia. While these parasites may have undergone a degree of adaptive radiation within the lake, there is little evidence of host specificity. Furthermore, a lack of reciprocal monophyly indicates that exchanges of microsporidia between Baikalian and non-Baikalian hosts have occurred frequently in the past and may be ongoing. Conversely, limitations to parasite exchange between Baikalian and non-Baikalian host populations at the margins of the lake are implied by differences in parasite prevalence and lack of shared microsporidian haplotypes between the two host communities. While amphipod hosts have speciated sympatrically within Lake Baikal, the parasites appear instead to have accumulated, moving into the lake from external amphipod populations on multiple occasions to exploit the large and diverse community of endemic amphipods in Lake Baikal.

1. Introduction

Adaptive radiation of host species into new ecological niches may allow them to escape from antagonistic interactions with parasites (Chew and Courtney, 1991), particularly where traits such as trophic specialisation reduce the likelihood of infection (Hablützel et al., 2017). Range expansions can also allow some host populations to escape from parasites (the 'enemy release' hypothesis) by moving into areas where the parasites do not occur (Keane and Crawley, 2002). Conversely, hosts may become susceptible to new parasites as a result of range expansion or evolutionary diversification (Bell and Burt, 1991). Both processes are therefore associated with turnover of parasite communities, as parasite species are lost and gained. Parasite turnover can itself become an important driver of host evolutionary diversification, as parasites reinforce reproductive isolation by selecting against hybrids or immigrants (Karvonen and Seehausen, 2012) and intensify sexual selection upon immunity traits (Eizaguirre et al., 2009). However, host diversification may also limit parasite prevalence because host species typically differ in their capacity to transmit any given parasite (Ostfeld and Keesing, 2012). A diverse community of host species is therefore expected to amplify a parasite less effectively than a less diverse community which contains a higher proportion of the optimal host species (the 'dilution effect') (Civitello et al., 2015).

Particularly useful insights into the effects of range expansions and adaptive radiations upon parasite diversity and prevalence can be provided by the study of species flocks within ancient lakes. While the vast majority of the world's lakes are no older than 10,000 years, approximately two dozen lakes are considerably older, by up to three orders of magnitude in some cases (Martens, 1997). These ancient lakes form habitat islands which contain diverse habitats but are accessible only to a limited range of freshwater species. Hence, they are characterised by internal adaptive radiations, producing 'flocks' of endemic species (Greenwood, 1984). The expansion of the range of a host species into an ancient lake and its subsequent adaptive radiation provide many opportunities for the loss and gain of parasites (Hablützel et al., 2017). Amphipod crustaceans are key benthic components of many lake ecosystems and have formed modest species flocks in the ancient lakes Ohrid (Macedonia-Albania), Titicaca (Peru-Bolivia), Issyk-Kul (Kyrgyzstan) and Fuxian Hu (China) (Gonzalez

☆ Nucleotide sequence data reported in this paper are available in the GenBank™ database under the accession numbers MG063275, MG063425–MG063426, MF399461–MF399471, MG062889–MG062893, MG029369–MG029394, MG027864–MG027893, MF428415, MF405266.

* Corresponding author. Fax: +44 (0)1970 622350.
E-mail address: jei@aber.ac.uk (J.E. Ironside).

https://doi.org/10.1016/j.ijpara.2017.10.003
0020-7519/

and Watling, 2003; Sket and Fiser, 2009; Wysocka et al., 2013). However, freshwater amphipods reach their greatest diversity by far in Lake Baikal, Siberia (Russia) (Macdonald et al., 2005) which contains 20% of all known non-marine amphipod species (Takhteev, 2000b).

At 25–30 million years old, Lake Baikal is one of the world's oldest lakes and the deepest, reaching depths of 1637 m and containing 20% of the Earth's surface liquid fresh water. The fauna of Lake Baikal can be divided between Baikalian species exclusive to Lake Baikal, and Siberian species with Palaearctic or Holarctic distributions (Kozhov, 1963). Adaptive differences between these two species complexes appear to prevent Baikalian species from invading surrounding bodies of water while excluding Siberian species from the main lake. This 'immiscibility' of Baikalian and Siberian species may be due to the unusual, super-oligotrophic conditions of the lake, which is characterised by low temperatures, high levels of dissolved oxygen (Timofeyev et al., 2010) and low levels of humic substances, allowing UV light to penetrate deeper and generate oxygen free radicals (Sommaruga and Psenner, 1997). It is proposed that, through becoming specialised to the unusual conditions of the lake, endemic Baikalian amphipods are able to competitively exclude more generalist Siberian species (Kozhov, 1963).

Molecular phylogenetic analysis suggests that endemic Baikalian amphipods arose by speciation within Lake Baikal following one or two colonisation events (Macdonald et al., 2005). Most Baikalian amphipods are restricted to the main lake, although some species penetrate the River Angara, Baikal's only outflow, and the lower parts of Baikal's various tributaries (Kamaltynov, 1999). Although certain endemic Baikalian amphipods such as *Gmelinoides fasciatus* have been introduced successfully to other parts of Russia, even these species have failed to extend their ranges away from the lake naturally (Berezina and Panov, 2004). Phylogenetic analyses consistently place the Siberian species *Gammarus lacustris* as a sister species to the Baikalian amphipod clade (Macdonald et al., 2005), suggesting that the common ancestor of the Baikalian amphipods was *G. lacustris* or a closely related species. *Gammarus lacustris* does not occur in the open lake and is restricted to nearby ponds, bays near the mouths of tributaries and portions of the lake cut off by sand bars (Kozhov, 1963).

Amphipods are hosts to a great diversity of microsporidian parasites, many of which can be transmitted vertically via the transovarial route (Cali and Takvorian, 2014). Some vertically transmitted microsporidian parasites of amphipods are feminisers, causing infected individuals to develop as females, whatever their genetic predisposition (Ironside et al., 2003). In theory, vertically transmitted parasites are expected to exhibit high levels of host fidelity and hence great likelihood of co-speciation (Smith, 2009), a prediction supported by the adaptation of vertically transmitted microsporidia to local populations of amphipods (Hatcher et al., 2005). On this basis it is expected that a co-evolutionary diversification of microsporidian parasites may have taken place in Lake Baikal, accompanying the adaptive radiation of their amphipod hosts.

Additionally, the cold, super-oligotrophic conditions within Lake Baikal may have provided opportunities for amphipods to escape from some microsporidian parasites. Vertical transmission, replication and feminization by amphipod microsporidia can all be affected by changes in temperature (Kelly et al., 2002; Dunn et al., 2006) and these effects can vary between species. Ecological specialisation also has the potential to have allowed Baikalian amphipods to escape from their parasites. Their common ancestor is likely to have been a generalist benthic detritivore and facultative predator such as *G. lacustris* (Hynes and Harper, 1972). While many Baikalian amphipods retain this generalist lifestyle, others have adapted to very different ecological niches, including the sponge epibiont *Dorogostaiskia parasitica* and the pelagic zooplanktivore *Macrohectopus branickii* (Kozhova and Izmesteva, 1998). Such radical changes in trophic ecology have the potential to select against microsporidian species which rely upon horizontal transmission via environmental spores and/or intermediate hosts.

Recent molecular studies indicate that microsporidia of Baikalian amphipods include the genera *Dictyocoela* and *Nosema* which also occur in European amphipod hosts (Kuzmenkova et al., 2008; Wilkinson et al., 2011; Madyarova et al., 2015). A large number of additional ssrRNA sequences from Baikalian amphipods have been submitted to GenBank, some of which have been putatively identified as belonging to the genus *Cucumispora*, which also infects amphipod hosts in Europe (Bojko et al., 2017). However, other microsporidian sequences from Baikalian amphipods bear no obvious relation to any described microsporidian species.

This study provides, to our knowledge, the first comparison of microsporidian diversity and prevalence between endemic amphipods within Lake Baikal and the closely related Holarctic species, *G. lacustris*. It also provides a phylogenetic analysis of the various microsporidia discovered in endemic amphipods of Lake Baikal, comparing them with those discovered in other amphipod species. These comparisons provide insights into the turnover in the microsporidian parasite community which has resulted from adaptive radiation of amphipod hosts within this ancient lake.

2. Materials and methods

2.1. Collection and storage

Amphipods were sampled from the shallow littoral zone (<2 m depth) of Lake Baikal, the outflowing River Angara, the tributary River Barguzin and nearby ponds using a hand net. All samples were collected from the southern part of the lake shore, including Olkhon Island (Table 1, Fig. 1). All sampled individuals were separated approximately into species by inspection and placed in 80% Ethanol for preservation during transport. More precise identification was performed in the laboratory (Takhteev, 2000a). In addi-

Table 1
Locations in Lake Baikal region, Russia, from which amphipods were collected.

Location	Latitude	Longitude	Habitat(s)
Lystvyanka	51° 50′ 34.8″ N	104° 52′ 33.6″ E	Lake Baikal and River Angara
Babushkin	51° 43′ 8.4″ N	105° 51′ 0″ E	Lake Baikal
Bolshoi Koty	51° 54′ 14.4″ N	105° 4′ 33.6″ E	Lake Baikal
Kultuk	51° 42′ 0″ N	103° 41′ 56.4″ E	Lake Baikal
Zabaikalsky National Park	53° 37′ 44.4″ N	109° 0′ 28.8″ E	Lake Baikal
	53° 36′ 39.6″ N	108° 58′ 51.6″ E	Ponds
Irkutsk	52° 9′ 46.8″ N	104° 9′ 46.8″ E	River Angara
	52° 8′ 34.8″ N	104° 11′ 9.6″ E	Reservoir
	52° 11′ 2.4″ N	104° 9′ 39.6″ E	Ponds
Barguzin	53° 21′ 50.4″ N	109° 22′ 55.2″ E	River Barguzin
Ust Barguzin	52° 14′ 42″ N	108° 35′ 31.2″ E	Lake Baikal
Olkhon Ferry	53° 0′ 43.2″ N	106° 33′ 18″ E	Lake Baikal
Yalga	53° 5′ 27.6″ N	107° 6′ 10.8″ E	Lake Baikal and Lake Khankhoy
Khuzhir	53° 7′ 19.2″ N	107° 12′ 7.2″ E	Lake Baikal

Please cite this article in press as: Ironside, J.E., Wilkinson, T.J. Accumulation and exchange of parasites during adaptive radiation in an ancient lake. Int. J. Parasitol. (2017), https://doi.org/10.1016/j.ijpara.2017.10.003