Competing invaders: Performance of two *Anguillicola* species in Lake Bracciano

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ABSTRACT

Anguillicola crassus is one of the most successful parasitic invasive species as it has spread from its original habitat in East Asia throughout the world and has acquired five new eel host species in the course of its invasion within the last three decades. Records from an Italian lake indicate that this species has even displaced an established population of its close relative *A. novaezelandiae* originating from New Zealand. In order to analyze the reasons for its high invasive potential, this review highlights recent studies, which substantiate the selective advantages of *A. crassus* over *A. novaezelandiae*.

Laboratory infection experiments revealed that *A. crassus* features a less synchronized development compared to *A. novaezelandiae* in the European eel, which enables this species to emit eggs over a longer period of time. Differences in the time period required for first egg output and in the maturation process of second stage larvae in intermediate hosts could also be detected, which may lead to differences in infection potential. Finally, microsatellite analyses have shown that hybridization processes are possible, but might only occur between *A. crassus* males and *A. novaezelandiae* females. Taken as a whole, the sum of minor selective advantages and differences in life cycle traits could have considerably contributed to a replacement of one species by the other.

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1. Introduction

As a most obvious sign of globalization, worldwide trade of goods and of live organisms has expanded appreciably. These activities often entail an intended or unintended introduction of non-endemic species into new habitats. Once introduced, just a few of these nonindigenous species (NIS) are capable of completing a successful invasion by establishing a stable population in the new habitat and spreading even further (Kolar and Lodge, 2001). The establishment of invasive species may have a considerable impact on the fitness of indigenous populations and even on biodiversity in general by causing major changes in the composition of species (McGeoch et al., 2010; Hatcher and Dunn, 2011). Invasive species comprise free-living organisms as well as parasites. Free-living invasive species serving as hosts can influence the new environment by either bringing in new parasite species, which are able to infect endemic free-living species (spillover; Strauss et al., 2012), by serving as a new host to endemic parasites (spillback) (Kelly et al., 2009), or by gaining an advantage over endemic species when losing originally associated parasites (enemy release) (Torchin et al., 2003; Hatcher and Dunn, 2011). Since both the affected ecosystem and the invader are influenced by one another, changes do not only apply to the new habitat, but also to the invasive organism. While free-living species have to meet the challenge of coping with unfamiliar environmental conditions, newly introduced parasites must find new intermediate and/or final hosts suitable for maintaining their life cycle. Additionally, they are involved in competitive interactions with both the already established parasite community of the new host as well as with the physiological (i.e. immune) responses of the hosts. Accordingly, one may assume that invasive parasites should have an advantage over other invasive parasite species if they feature a simple (monoxenic) life cycle with low host specificity, so that they can potentially infect a wide range of new available hosts.

In contrast, one of the most successful parasitic invasive species world-wide is the heteroxenic swim bladder nematode *Anguillicola crassus* (synonym *Anguillicoloides crassus*, see Laetsch et al., 2012), which is an indigenous parasite of the Japanese eel (*Anguilla japonica*) in Asia, and was introduced to Germany in the 1980s (Neumann, 1985) from where it spread throughout the population of the European eel (*Anguilla anguilla*).

To this day, this parasite was recorded as a nonindigenous species on three continents and in five eel species (Neumann, 1985; Johnson et al., 1995; Moravec, 2006; Sasal et al., 2008). It even seemed to

have outcompeted the closely related species *Anguillicola novaezelandiae* (a native parasite to *Anguilla australis* in Australia and New Zealand) in an isolated lake in Italy. *A. novaezelandiae* was introduced in the 1970s into Lake Bracciano and established a stable population in the European eels of the lake. After *A. crassus* had been introduced into the lake, both parasite species were recorded simultaneously in 1993, but no mixed infections of European eels were found. In 2004, *A. crassus* was the only *Anguillicola* species found in the lake (Paggi et al., 1982; Moravec et al., 1994a; Münderle, 2005).

According to the limited number of studies about *A. novaezelandiae*, it does not cause any swim bladder damage in the European eel, in contrast to *A. crassus*, which is more virulent and reaches higher infection intensities in the new eel host (Paggi et al., 1982; Moravec et al., 1994a; Münderle, 2005; Moravec, 2006) with severe effects on swim bladder histology and function (Molnár et al., 1993; Molnár, 1994; Würtz et al., 1996; Würtz and Taraschewski, 2000; Barry et al., 2014). However, it remains unclear why the less pathogenic nematode disappeared, whereas its conspecific establishes at every new location. This leads to the question why *A. crassus* is a more successful invader and what are its advantages compared to its close relative, which was not able to establish as an invasive species. The present article gives detailed insights into this unique situation and points out possible reasons allowing *A. crassus* to outcompete its close relative.

2. *Anguillicola* in Lake Bracciano

Lake Bracciano is an almost round lake northwest of Rome, Italy, without in- or outlet. European eels are regularly introduced into the lake to maintain supplies for fishing (Moriarty and Dekker, 1997). Swim bladder parasites of the genus *Anguillicola* were first recorded in Lake Bracciano by Paggi et al. (1982). The authors originally identified the species as *Anguillicola australiensis*, but Moravec and Taraschewski (1988) identified the species as *A. novaezelandiae* in their review on the genus *Anguillicola*. The nematodes were introduced to the lake in 1975 along with their original host species *A. australis* from New Zealand (Welcomme, 1981; Paggi et al., 1982). While *A. novaezelandiae* established as a non-indigenous parasite of the indigenous European eel (*A. anguilla*) in Lake Bracciano and never spread outside the lake, a closely related species was introduced to Europe. In spring of 1982, *A. crassus*, an indigenous parasite of the Japanese eel (*A. japonica*) in Asia, was first recorded in European eels of the Weser-Ems-Region in Germany (Neumann, 1985). Soon after this first record, the parasite began its rapid spread throughout the population of the European eel on the European continent as well as in North Africa as a consequence of natural eel movements and especially eel trade (Kennedy and Fitch, 1990; Kirk, 2003; Moravec, 2006; Taraschewski, 2006; Jakob et al., 2009). But the triumph of *A. crassus* continued when the parasite was recorded in American eels (*Anguilla rostrata*) in North America in 1995 (Johnson et al., 1995) and in three African eel species on the Island of Reunion in 2005 (Sasal et al., 2008). The parasite raised attention as early as 1979, when Egusa (1979) noted that naïve European eels suffer more from an infection with *A. crassus* in Asian aquaculture than the Japanese eel as the original host. But the warnings of the author to prevent the introduction of the parasite to Europe went unheard and still the worldwide trade with live eels is going on.

In October 1993, *A. crassus* and *A. novaezelandiae* were both recorded in European eels of Lake Bracciano (Moravec et al., 1994a). This was a very unique finding of two *Anguillicola* species in a single eel species, though no mixed infections in individual eels were found. Similarly, this was the last record of *A. novaezelandiae* in the lake. Between November 2002 and September 2004, Münderle (2005) sampled European eels of Lake Bracciano, but identified all *Anguillicola* individuals as *A. crassus* based on morphological features as well as

on allozyme analyses, which suggests that *A. novaezelandiae* became extinct from the lake.

## 3. Two of a kind?

3.1. Anguillicola crassus

After its introduction to Europe and its spread throughout the European eel population, *A. crassus* became of significant interest. Compared to the Japanese eel, the European eel has no effective immune response against the parasite (Knopf and Mahnke, 2004; Knopf, 2006; Knopf and Lucius, 2008). This leads to a high prevalence of up to 100 % as well as a high infection intensity in European eel populations compared to findings in the original habitat in Asia, where recordings indicate a prevalence ranging from 17 to 56 % with relatively low intensities (Nagasawa et al., 1994; Jakob et al., 2009). Combined with other stressors like low oxygen levels in the water, a high fish population density, and the presence of insecticides, *A. crassus* even caused mass mortalities of eels in Lake Balaton (Hungary) and the Morava River system (Czech Republic) (Molnár et al., 1991; Baruš et al., 1999; Nemcsók et al., 1999; Lefebvre et al., 2012). As a result, the parasite was intensively studied both in wild eels (overview see Jakob et al., 2009) and in experimentally infected eels (Haenen et al., 1989, 1991, 1996; De Charleroy et al., 1990a; Moravec et al., 1994b; Knopf et al., 1998; Ashworth and Kennedy, 1999; Knopf and Mahnke, 2004; Fazio et al., 2008; Weclawski et al., 2013).

The basic life cycle of the species is rather simple (see Fig. 1): Adult nematodes of this species settle in the swim bladder of eels, nourish on blood, mate and produce eggs with second stage larvae (L2). Through excretion, L2 are released into the water, where they are ingested by intermediate hosts (mostly copepods). Inside the copepod, larvae develop from the second to the third larval stage (L3). As soon as L3 are ingested by the final host (eel), the larvae penetrate its intestine in order to reach the swim bladder wall, where they molt into the fourth stage larvae (L4). L4 grow further, molt, enter the swim bladder lumen and develop into adult nematodes (Køie, 1991; Kirk, 2003; Moravec, 2006; Kennedy, 2007).

Experimental infection studies of (potential) intermediate hosts revealed almost 20 suitable species in Europe, mainly cyclopoid copepods (overview see Moravec, 2006). Additionally, paratenic hosts were found to be facultatively involved in the life cycle of *A. crassus* in Europe. More than 30 fish species, but also tadpoles, as well as some aquatic invertebrates, have been recorded as paratenic hosts (De Charleroy et al., 1989, 1990b; Thomas and Ollevier, 1992; Haenen et al., 1994; Moravec and Konecny, 1994; Pazooki and Székely, 1994; Székely, 1994; Moravec, 1996; Moravec and Skorikova, 1998). The blood-sucking feeding habit of adult parasites can lead to severe changes of the swim bladder wall tissue and to loss of lumen, both resulting in an impairment of the buoyancy regulation of the host (Molnár et al., 1993; Molnár, 1994; Würtz et al., 1996; Barry et al., 2014). As a consequence of parasite infection, eels with impaired swim bladders may be unable to reach their spawning grounds in the Sargasso Sea (5500 km transoceanic migration) (Sures and Knopf, 2004; Palstra et al., 2007).

3.2. Anguillicola novaezelandiae

Even though *A. novaezelandiae* was introduced to Lake Bracciano as early as 1975, it was first recorded seven years later (Paggi et al., 1982). Since data of its occurrence are only sparse, one can only speculate whether the parasite may have been introduced several times or only once (Moravec, 2006). Until the description of the species and the revision of the genus by Moravec and Taraschewski (1988), records of the species were mentioned as *A. australiensis* or maybe even *A. crassus* and a precise species determination is therefore often
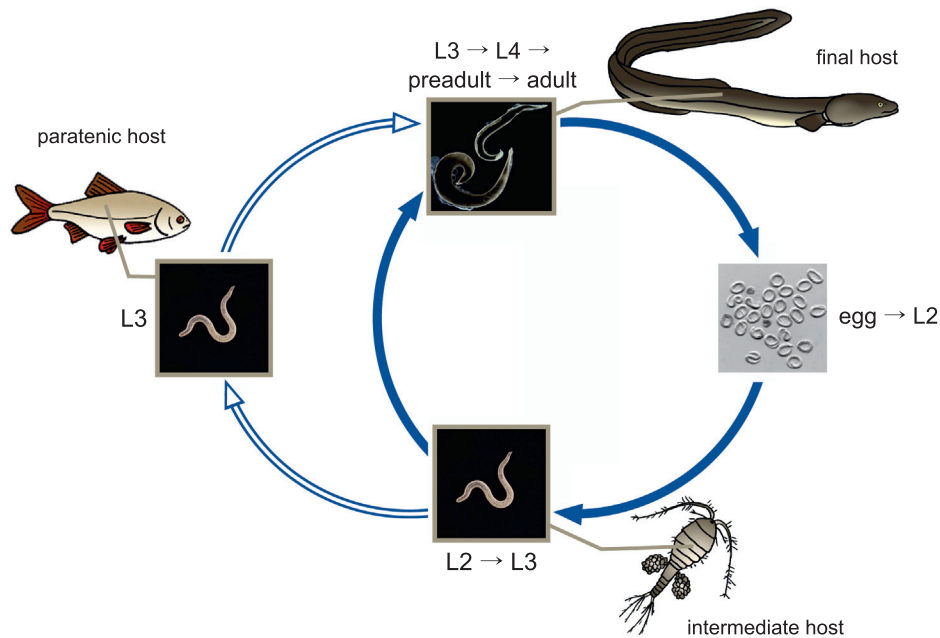
Fig. 1. Life cycle of *Anguillicola crassus*. The basic life cycle (*blue arrow*) includes eels as final hosts and copepods as intermediate hosts. By integrating additional paratenic hosts (e.g. fish), the life cycle can be extended (*white arrow*).*Source:* (Moravec, 2006).

not clear. Records of *A. australiensis* in European eels in Italy during the 1980s could possibly be *A. novaezelandiae* (Saroglia et al., 1985; Di Cave, 1986; Sarti, 1986).

Moravec et al. (1994a) conducted experimental infections of the copepod species *Cyclops strenuus* successfully with L2 of *A. novaezelandiae* originating from Lake Bracciano from October 1993 and studied the life cycle and morphology of the species in the intermediate and final host. These as well as other authors did not record any swim bladder damages due to *A. novaezelandiae* infections in any eel species (Paggi et al., 1982; Moravec et al., 1994a; Münderle, 2005). Addtitionally, the detailed experimental infection study of Dangel et al. (2013) revealed great differences in the development of *A. novaezelandiae* in European eels compared to *A. crassus*. While *A. novaezelandiae* matures in a synchronized fashion and eggs containing L2 were found 120 days post infection at the earliest, the development of *A. crassus* is less uniform, so that eggs are emitted earlier and over longer time periods. Furthermore, infrapopulations of *A. crassus* seem to be regulated by density, whereas no density-dependent effects for *A. novaezelandiae* could be recorded, even when the number of administered larvae was doubled (40 instead of 20), it did not noticeably change the maximum adult population size (Fazio et al., 2008; Dangel et al., 2013; Weclawski et al., 2013).

Although there is no information about the range of intermediate or paratenic hosts so far, fundamental differences to *A. crassus* do not appear to be likely. In its endemic range in New Zealand, *A. novaezelandiae* seems to show a seasonal pattern, which is a unique finding for a species of the genus (Dangel and Sures, 2013).

4. Survival of the fittest – why could *A. crassus* predominate in Lake Bracciano?

The knowledge on species of the genus *Anguillicola* is mainly dominated by studies of *A. crassus* and discoveries on this species were often thought to be assignable to the other species. Recent studies on *A. novaezelandiae* revealed great differences in its life cycle compared to *A. crassus* (Dangel et al., 2013). While the non-uniform growth of *A. crassus* will lead to a production of L2 over a

longer period of time, an equally big infrapopulation of *A. novaezelandiae* will produce eggs over a shorter period. Therefore, infective stages of *A. crassus* are present in the environment over a longer period of time, compared to *A. novaezelandiae*. A longer period until the first egg output occurs as well as a synchronized development with shorter periods of L2 emission could have been a disadvantage for *A. novaezelandiae* in Lake Bracciano. Whether females of one of the species may produce more eggs than the others has not been studied yet.
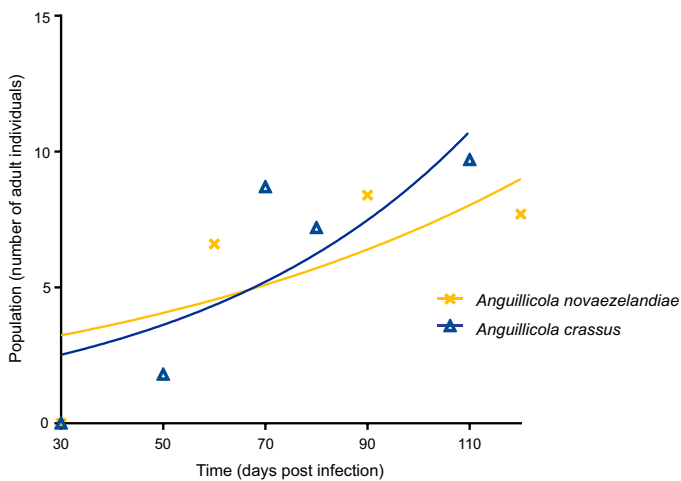
For analyzing differences in population growth rates of the two *Anguillicola* species, we developed a model constructed on the basis of recovery data from two infection studies. We used data on experimental infections from *A. crassus* from Knopf et al. (1998) and *A. novaezelandiae* from Dangel et al. (2013). Both data sets were comparable in terms of infection doses and water temperature. According to these data, at 120 days post infection, the number of adult individuals per eel is less than ten. Therefore, it can be assumed that during this period, the population growth of parasites expressed by the number of adult individuals per host is not limited by the capacity of the host. In this respect, the mean number of adult individuals per host can be expressed by the following equation:

$$N_t = N_0 \times e^{r \times t}$$

where N_t is the number of adults per host at t days post infection, N_0 is the number of parasites in one host on the day of infection, and t (days) is the number of days post infection.

The population growth rate (expressed by the change in the number of adult individuals per host per day) was determined by fitting the developed equation to the experimental data. From this it followed that *A. crassus* was found to have a higher population growth rate ($r = 0.018$; $r^2 = 0.68$) than *A. novaezelandiae* ($r = 0.011$; $r^2 = 0.54$) (Fig. 2). The modeled growth rates of the two species indicate that *A. crassus* might have a general advantage over *A. novaezelandiae* as the former parasite species features a sharper increase in adult population compared to the latter one within the same period of time.

In an unpublished study on the development of both *Anguillicola* species in copepod intermediate hosts, Dangel, Keppel, Caspers and

Fig. 2. Population growth rate. The relationship between the number of adult individuals per host and the days post infection is shown. The lines represent model predictions and the dots represent experimental data.

possible (which were not detected in field studies in Lake Bracciano), but could also find eggs of hybrid origin. Females of *A. novaezelandiae* contained eggs fertilized by *A. novaezelandiae* as well as by *A. crassus* males. The examined eggs of *A. crassus* females on the other hand only contained *A. crassus* specific microsatellite markers. Grabner et al. (2012) only analyzed eggs, so it is still not clear whether hybrids are viable or fertile. Nevertheless, this could be a possible explanation for the disappearance of *A. novaezelandiae* in Lake Bracciano. *A. crassus* genes could have quickly dominated the *Anguillicola* population, for *A. novaezelandiae* males seem to be incompatible with *A. crassus* females but not vice versa. Even if the hybrid offspring is not viable, this would have been a selective disadvantage for *A. novaezelandiae*. Similar cases of incomplete reproductive separation of closely related parasite species have been found already for other helminths. For example *Fasciola hepatica* and *Fasciola gigantica* formed hybrid offspring in a laboratory experiment (Itagaki et al., 2011) and *Schistosoma intercalatum* was completely replaced there by the introduced *Schistosoma haematobium* due to introgressive hybridization in Cameroon (Tchuem Tchuenté et al., 1997).

5. Conclusions

The advantage of a higher population growth rate might have substantially contributed to a more successful establishment of *A. crassus* in Lake Bracciano compared to *A. novaezelandiae*. Hybridization between *A. crassus* males and *A. novaezelandiae* females may have also been one way of allowing *A. crassus* to outcompete *A. novaezelandiae* in the lake. Nevertheless, it is conceivable that differences in life cycle traits also played a key role in the predominance of *A. crassus* in the lake. Further research should be performed to gain more insights into the disappearance of *A. novaezelandiae*. The worldwide success of *A. crassus* as an invasive species is also promoted by the massive trade of live eels. *A. japonica, A. anguilla*, and *A. rostrata* as original and new host species of *A. crassus* are at the same time the top three eel species for food production and trade world-wide, both processed and alive (FAO, 2012). This provides the parasite the opportunity to be distributed around the world and into new habitats.

Sures found significant differences in the duration of L3 development (see Fig. 3). The experiment was performed with cyclopoid copepods as described in Dangel et al. (2013) and the development of *Anguillicola* larvae was checked daily. At 20 °C, *A. crassus* developed within 14–25 days, while L2 of *A. novaezelandiae* required 16–32 days to mature to infective third stage larvae. This is again an obvious advantage for *A. crassus* in an environment where both species compete for the same resources.
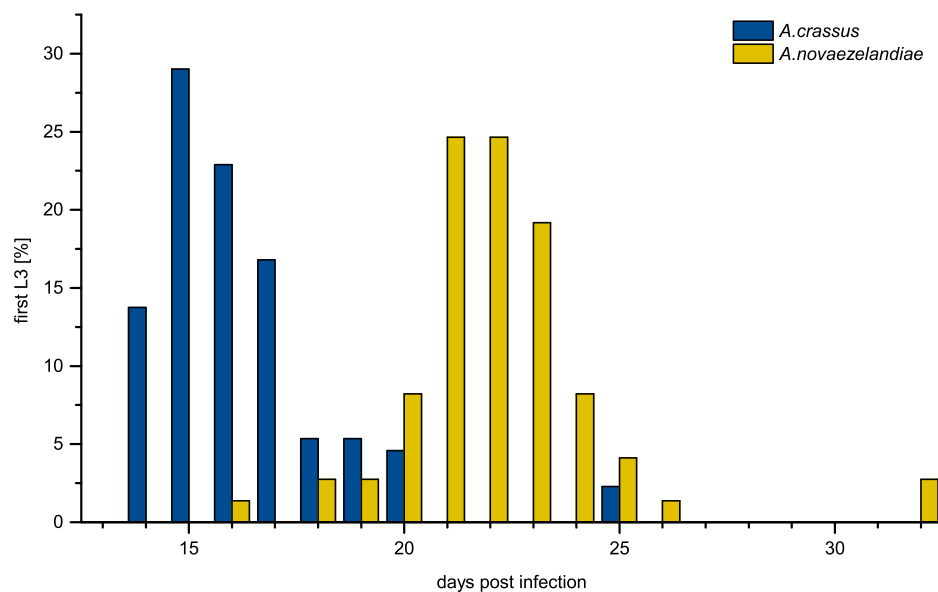
If we assume that both *Anguillicola* species develop in the same copepod species, a slower development to L3 would mean a further disadvantage for *A. novaezelandiae* compared to *A. crassus*. Therefore, selection could also have taken place on intermediate host level.

However, the findings of Grabner et al. (2012) suggest another possible way of replacement. In an infection experiment with both *Anguillicola* species in one eel, and subsequent analysis of microsatellite patterns of parent and offspring, the authors did not only provide a proof that mixed infections of European eels are

Fig. 3. Development to L3 in intermediate host. Days post infection (dpi) until *Anguillicola* spp. larvae develop into the infective L3 at 20 °C. Most *A. crassus* larvae develop within 17 dpi while the majority of *A. novaezelandiae* larvae need 23 dpi to complete the development in the intermediate host.

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Conflict of interest

The authors declared that there is no conflict of interest.

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