Lack of evidence for European eel infection by *Anguillicola crassus* in Madeira Island, Macaronesia

Anguillicola crassus in eels of Madeira

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Acknowledgements

The Portuguese National Funds supported this work through ARDITI – *Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação*, within IO Post-Doctoral research grant (M1420-09-5369-FSE-000002). This study also had the support of FCT – Fundação para a Ciência e a Tecnologia, I.P., through the strategic project UIDB/04292/2020 awarded to MARE, through project LA/P/0069/2020 granted to the Associate Laboratory ARNET, and within I&D units grants. JCC is funded by national funds through FCT under the Scientific Employment Stimulus Institutional Call—(CEECINST/00098/2018).

We thank fishermen and the regional *Direção Regional do Mar* for the specimens; and Anaïs Esposito and colleagues for sharing data regarding *A. crassus* distribution.

Data availability statement

The data supporting the findings of this study are available upon request.

Conflict of interest

The authors declare to have no conflict of interest.

Ethical considerations

No eels were intentionally sacrificed for this study. All specimens had been caught during recreational fishing or delivered to our research institute by the Regional Department for the Sea. Specimens were transported with the permission of the regional Institute for Forestry and Nature Conservation (*Instituto das Florestas e da*

Conservação da Natureza; IFCN) – transport authorisations 03/IFCN/2021 - FAU MAD and 02/IFCN/2023 - FAU MAD.

Introduction

Anguillicola crassus (Kuwahara, Niimi and Itagaki, 1974) is a nematode that parasitises the swimbladder of anguillid eels (Gollock et al., 2005). Although it originated in East Asia, where it is endemic to its native definitive host, the Japanese eel (*Anguilla japonica*), this parasite has rapidly colonised non-native areas (El-Shehabi et al., 2018; Lefebvre et al., 2012). Its invasive success can be partially explained by its high tolerance to ecological factors such as temperature and salinity, and the ability of its larvae to survive outside the host (Taraschewski, 2006; Kennedy, 2007). Infection success depends on only an intermediate and a final host within which to reproduce and complete its life cycle, however this parasite can infect a wide range of paratenic hosts – including ostracods, insect larvae, gastropods, amphibians, and fish (e.g. De Charleroy et al., 1990; Kirk, 2003; Thomas & Ollevier, 1992). This nematode is an obligate parasite whose specificity relies solely on its final host, i.e., eels of the genus *Anguilla* (Sures, 1999).

Anguillids are catadromous species that reproduce in the open ocean and larvae migrate with ocean currents to colonise continental waters. Eels are infected by *A. crassus* during continental life stages (Van Banning & Haenen, 1990). Parasite larvae enter the digestive tract of eels after ingesting infected intermediate or paratenic hosts (Kennedy, 2007). Larvae then migrate to the swimbladder where they develop into adults and reproduce. Except for its natural host *A. japonica*, most anguillids are highly sensitive to parasitic infections from this nematode (Egusa, 1979). This is particularly the case for the panmictic European eel *Anguilla anguilla* (Linnaeus) that hatches in the Sargasso Sea and has a distribution range covering much of Europe, North Africa and the Atlantic islands (Als et al., 2011; Tesch, 2003). The introduction, spread and

pathogenic effects of *A. crassus* have contributed to the Critically Endangered conservation status of *A. anguilla* (ICES, 2022; Pike et al., 2020).

A. crassus infections can reduce the fitness of *A. anguilla* and its survival under stressful ecological conditions such as hypoxia (e.g., Molnár, 1991; Gollock et al., 2005). In addition, haematophagy by *A. crassus* – with consequent thickening of the swimbladder epithelium, loss of elasticity and reduction in gas volume (Van Banning & Haenen, 1990; Kennedy, 2007) – may impair the hydrostatic capacity of this organ thereby reducing the eel swimming performance (Barry et al., 2014). Thus, this parasite-induced impact on the buoyancy of the eel's swimbladder – essential for the diel vertical migrations they perform during their reproductive migration (Aarestrup et al., 2009) – may jeopardise the success of silver eels in reaching the spawning area (Palstra et al., 2007). This parasite was probably introduced into Germany in the early 1980s with the import of live eels from Taiwan (Koops & Hartmann, 1989). From here and over the ensuing two decades, the trade in eels for consumption, aquaculture and restocking programs resulted in multiple introductions and the spread of this parasite across Europe and North Africa (Wielgoss et al., 2008; Jakob et al., 2016). After its introduction into an aquatic system, the dynamics of infection of European eel by *A. crassus* follows a common pattern that includes an initial period characterised by a rapid increase in prevalence, intensity and abundance (for infection terminology see Bush et al., 1997), until it peaks and tends to stabilise over a few decades (Lefebvre & Crivelli, 2004; Unger et al., 2024). This is a major concern because once introduced there is no way to eradicate the parasite (Lefebvre & Crivelli, 2004).

Although the swimbladder parasite is present in most habitats colonised by European eel subpopulations (Esposito et al., 2023a), some regions remain unstudied. This study investigates the infection of eels and their body condition on Madeira Island,

part of the poorly studied Macaronesian distribution of European eels. We hypothesized that *A. crassus* is not present on the island as there are no official records of international eel trade. Therefore, the swimbladders of eel inhabiting this island are theorized to be in good condition. Any absence of infection may also contribute to eels presenting good condition factors.

Materials and Methods

The Madeira archipelago is isolated from mainland Europe and North Africa more than 700 km away (Figure 1a). Madeira – its largest island (741 km^2) – has more than 200 streams containing extensive established populations of one native fish *A. anguilla* (Marques, 1994; Órfão et al., 2024). Between April 2021 and March 2023, nineteen eels were caught at four sites in three streams of this Island (Figure 1b). Eels were frozen and later thawed and dissected to determine life stage, sex, age, body condition, and infection status with *A. crassus*.

Morphological traits were recorded to determine life stage based on Durif et al.'s silver index (SI; 2009). These include total weight (TW) measured to the nearest 1 g, and total length (TL), pectoral fin length (FL), and horizontal and vertical eye diameters (DH and DV) measured to the nearest 1 mm. Sex was identified based on visual inspection of the gonads of the dissected eels (Beullens et al., 1997). The sagittal otoliths were removed, cleaned and stored in tubes for later analysis. Age was determined using the method of clearing whole otoliths in 96% ethanol (ICES 2009, 2011). Three independent readers analysed and counted the number of rings on each otolith under a stereomicroscope. The body condition was estimated based on Fulton's condition factor ($K = TW\ (g) \times 100) / TL\ (cm)^3$; Fulton, 1904). Finally, swimbladders were examined macroscopically to inspect for the presence of *A. crassus*, signs of

previous infection and damage – i.e., pigmentation caused by the parasite blood feeding or exudates due to inflammation. A Swimbladder Degenerative Index (SDI) was calculated by summing three scored criteria: organ transparency, thickness, and pigmentation/exudate – scored from 0 to 2 (Lefebvre et al., 2002). The SDI values range from 0 to 6, where "0" is no sign of infection and "6" is a severely affected swimbladder.

Results

All captured eels were females between 3 and 7 years (Table 1). Their total body length varied between 359-636 mm (508 mean ± 84 SD), their body weight between 78.7-542.8 g (276.0 mean ± 139.2 SD), and Fulton's condition factor between 0.15 and 0.24 (0.19 mean ± 0.03 SD). Twelve eels were classified as resident (stage FII), five were pre-migrant (FIII), and two were migrant (FV), i.e. eels that will start their spawning migration.

No *A. crassus* nematodes were found, nor were there any exudates in the swimbladder lumen or pigmentation on the wall of this organ. The SDI ranged between '0' (intact organ with no signs of pathology; n = 16) and '3' ('moderately damaged' according to Lefebvre et al., 2002; n = 3). SDI of three swimbladders was greater than zero, although having no pigmentation or exudates. However, these organs had a thicker and, therefore, an opaque wall.

Discussion

Invasive pathogens are a major threat to wildlife (Smith et al., 2009). This is the case of *A. crassus* and the endangered *A. anguilla* (Esposito et al., 2023a; Kennedy, 2007; Kirk,

2003). In this first assessment of the parasite on an island in the Macaronesia region, our results suggest that European eels inhabiting the inland waters of Madeira are not infected with this invasive nematode. Therefore, these results seem to align with previous findings from Iceland, where – for the time being – European eels also seem to be free of *A. crassus* (Kristmundsson & Helgason, 2007). This is likely a consequence of both Madeira and Iceland being isolated from mainland areas to which the parasite was introduced and to the absence of its main introductory vector route: eel trade (Kennedy & Fitch, 1990). Despite these promising findings, swimbladder characters and eel body condition results deserve a deeper discussion and reinforce the need for future studies.

Although all swimbladders had a healthy appearance, three were classified as moderately damaged according to Lefebvre et al. (2002). This may be due to the subjectivity of the opacity and thickness criteria used in the SDI index (Lefebvre et al., 2011). Furthermore, opacity and thickness are highly correlated. As such, the increased vascularisation and thickness of the swimbladder wall during the silvering (Pelster, 2015) may lead to the apparent contradiction between SDI and the absence of parasites. Similarly, one of the two silver eels caught in November presented a very thick organ, and most eels with SDI superior to zero were in an advanced stage of silvering. Therefore, the few intriguing results are likely more reflective of the method's limitations (particularly associated with eels transforming into migrants), than indicate of missed infections.

Eels evaluated for this study were in good body condition. Although the absence of the parasite can contribute to this fitness parameter, the condition factor did not surpass others from subpopulations in the mainland where the parasite is present (e.g., Esposito et al., 2023b; Haenen et al., 2010; Durif et al. 2009). This aligns with mounting

evidence suggesting that eel infection by *A. crassus* and body condition are not correlated (e.g., Esposito et al., 2023b; Haenen et al., 2010; Myrenås et al., 2023). Future research should consider a deeper integrative approach to the fitness of *A. anguilla*, assessing the health status of eel spawners in particular. This could be done by looking for other pathogens, and by analysing fecundity and energy reserves (e.g., body fat levels, hepatosomatic index; Bourillon et al., 2020).

Regions where some of the critical threats to the European eel are absent have the potential to represent a stronghold for its conservation. This may be the case for Iceland and Macaronesia islands where geographical isolation and lack of international eel trade reduced the likelihood of invasion by *A. crassus*. Nevertheless, the introduction of this invasive nematode is plausible if species such as cyclopoid copepods which can act as intermediate hosts, or waters where such species are present, are introduced into watercourses (Sługocki et al., 2023; De Charleroy et al., 1990). Importantly, insular freshwater ecosystems are particularly sensitive to biological invasions (Leclerc et al., 2018; Simberloff, 1995). Therefore, it is prudent to survey for *A. crassus* presence in the Atlantic islands through eel swimbladder inspection and using eDNA and qPCR analyses (De Noia et al., 2022; Jousseaume et al., 2021).

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Tables

Table 1. *Anguilla anguilla* specimens caught in streams of Madeira Island and inspected for parasitism by *Anguillicola crassus*. Eels were collected from three streams on Madeira Island in different seasons and years. The following traits were recorded for each eel: total length (TL), total weight (TW), life stage, sex, silver index (SI), Fulton's body condition factor (K), age, swimbladder thickness, transparency, pigmentation and Swimbladder Degenerative Index (SDI).

Figure legends

Figure 1. a) Distribution of *Anguillicola crassus in* the spatial range of *Anguilla anguilla* (adapted from Esposito et al., 2023a). The recruitment areas of *A. anguilla* are marked in yellow (based on Righton & Metcalfe 2011). *A. crassus* has been detected in countries coloured in blue but not in light yellow, and remain to be studied in those in grey (based on Bychkova et al., 2022; Esposito et al., 2023a; Jakob et al., 2016; and Tkachenko et al., 2023). b) Sites in Madeira Island where eels were caught are represented by circles.

Author contributions

Órfão I.: research conceptualisation, data collection, writing (original draft preparation); **Monteiro R.**: data collection; **Portela T.**: data collection; **Almeida S.**: figure conceptualisation and design; **Rocha R.**: research conceptualisation, supervision; **Canning-Clode J.**: research conceptualisation, supervision, funding; **Domingos I.**: research conceptualisation, validation, supervision.

All authors contributed critically to this draft and gave final approval for publication.