Vol. 60: 133–139, 2004 | DISEASES OF AQUATIC ORGANISMS
Dis Aquat Org | Published August 9

Influence of *Anguillicola crassus* (Nematoda) and *Ichthyophthirius multifiliis* (Ciliophora) on swimming activity of European eel *Anguilla anguilla*

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ABSTRACT: We investigated the swimming activity of 70 European eels *Anguilla anguilla* in relation to natural infection with 2 parasite species: the eel-specific swimbladder nematode *Anguillicola crassus* and the non-specific skin and gill protozoan *Ichthyophthirius multifiliis*. We measured how long individual eels exposed to a water current in a swimming channel with a steady-stream profile could withstand the water current. The parasites affected the swimming behaviour of eels in different ways. The maximum period of time the fish were able to swim against the current was not correlated with infection by *A. crassus*. In contrast, infection with *I. multifiliis* reduced the swimming time. The protozoan has a higher pathogenicity than the swimbladder nematode, at least in closed systems, where *I. multifiliis* is able to spread within a few days. Reduction in swimming capacity after infection with the ciliate averaged 47 % compared to capacity prior to infection. Thus, our results do not support the previously suggested strong negative relation between swimming activity of eels and intensity of *A. crassus* infection, at least in the short-term. However, there are indications in the literature that the pathological effects of *A. crassus* on the eel swimmbladder may involve a higher energy demand, possibly manifested in a prolonged spawning migration. As a result, eels heavily infected with this parasite may arrive too late at the spawning site to participate in mating. This could ensure a selection of 'good genes'.

KEY WORDS: Swimming activity · European eel · *Anguilla anguilla* · *Anguillicola crassus* · *Ichthyophthirius multifiliis* · Pathology · Pathogenicity · Behaviour · Sexual mate choice

INTRODUCTION

The swimbladder nematode *Anguillicola crassus* (Dracunculoidea: Anguillicolidae) is an eel-specific parasite, introduced into Europe from Eastern Asia, where the Japanese eel *Anguilla japonica* serves as the natural definitive host (Moravec & Taraschewski 1988, Køie 1991, Kennedy 1993a,b). The first occurrence of *A. crassus* in Germany was recorded in 1982 (Neumann 1985). Since then, the parasite has successfully spread through Europe and attained high prevalences and intensities within populations of the indigenous European eel *Anguilla anguilla* (Taraschewski et al. 1987, Moravec & Taraschewski 1988, Moravec 1992, Würtz et al. 1998, Sures et al. 1999a). The parasite has also colonized populations of the European eel in North Africa (Maamouri et al. 1999) and spread to North America, where *Anguilla rostrata* was adopted as the final host (Johnson et al. 1995). In addition to the numerous reports on the biology and development of *A. crassus* in European eels and in the intermediate and paratenic hosts of the parasite (Egusa 1979, De Charleroi et al. 1990, Kennedy & Fitch 1990, Bonneau et al. 1991, Thomas 1993, Knopf et al. 1998), there has also been an interest in the adverse effects of this parasite on its host (e.g. Moravec & Konecny 1994, Székely 1994, Sures et al. 1999b). Histopathological studies have been conducted which have demonstrated thickening of the swimbladder wall, inflammation, infiltration of white blood cells, fibrosis, changes in the epithelial cells in infected swimbladders and altered gas compositions of this hydrostatic organ (Hartmann 1989, Van Banning & Haenen 1990, Molnár 1993, 1994, Molnár et al. 1995, Würtz et al. 1996, Würtz

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& Taraschewski 2000). Furthermore, the physiological and immunological responses of eels against *A. crassus* have been investigated (Nielsen & Buchmann 1997, Kelly et al. 2000, Knopf et al. 2000a,b, Sures et al. 2001, Sures & Knopf 2003). According to these studies it seemed likely that eels with severe swimbladder alterations are incapable of migrating to their spawning grounds (Würtz et al. 1996). Sprengel & Lüchtenberg (1991) reported that eels infected by *A. crassus* were handicapped in swimming compared to uninfected controls, and speculated whether these eels would be able to reach the Sargasso Sea.

We performed swimming experiments using eels naturally infected with *Anguillicola crassus* to check whether their swimming ability is affected by the nematode. The swimming ability of eels was also investigated using fish parasitised by the protozoan *Ichthyophthirius multifiliis*. The rapid life cycle and the enormous reproduction of the trophozoite stages of this pathogenic generalistic parasite result in massive infection pressure in closed systems such as aquaria. Under these conditions *I. multifiliis* may lead to mass mortality if not treated (Limanskii et al. 1984, Ewing & Kocan 1987, Ewing et al. 1988, Schmahl et al. 1992, Scholz 1999).

The aim of the present study was to determine the maximum swimming period of eels infected with *Anguillicola crassus*, from which we could determine whether infection by this neozoic parasite is likely to prevent the eels from reaching their spawning grounds in the Sargasso Sea. Uninfected eels and eels infected with a highly pathogenic ectoparasite (*I. multifiliis*) served as controls.

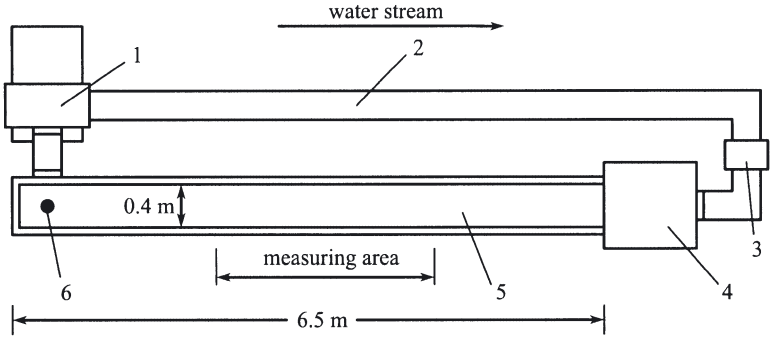

Fig. 1. Schematic of swimming channel. 1: pump; 2: polypropylene-pipe; 3: inlet bend; 4: rectifier chamber; 5: swimming channel; 6: outlet bend. Total length of swimming channel (5) = 6.5 m; rectangular cross-section = 0.4 m wide, 0.5 m deep. Two 10 mm quartz discs were fixed in measuring area to allow good view of fish (*Anguilla anguilla*) behaviour. Additional tube installed within measuring area guaranteed steady-stream profile during swimming performance of each eel. Water passed through swimming channel and outlet bend (6) and was subsequently pumped through polypropylene pipe (2) to the bend on the other side of the pipe (3), from where it passed back into swimming channel

MATERIALS AND METHODS

Experimental design. We collected 70 eels (40.3 ± 2.7 cm, 81 ± 16 g) from the River Weser by electrofishing in May 2000. Eels were kept individually in 30 to 60 l compartments, equipped with a polypropylene tube to provide a refuge. For the swimming experiments, individual eels were placed in a swimming channel (Fig. 1). A tube was installed within the channel that guaranteed a constant-stream profile as well as a constant current of 0.62 m s^{-1}, as monitored by a flow meter. The swimming activity of each eel was measured against the current with a stopwatch. Every eel was made to swim 3 times in the channel with a 2 d recovery phase between each trial. The maximum period of swimming was recorded for each eel. Swimming was considered to end when an eel passively drifted with the current into a net at the end of the tube. If eels swam longer than 10 min against the current, the experiment was stopped.

Additionally, the swimming activity of eels prior to and following infection with *Ichthyophthirius multifiliis* was recorded. Eels that had already been used for the swimming experiments were randomly selected and maintained together with eels naturally infected with *I. multifiliis*; 4 d post-infection, the eels infected in this manner were then re-introduced into the swimming channel.

At the end of the experiments all eels were killed, measured, weighed and immediately examined for parasites according to standard protocols (e.g. Sures & Streit 2001). All adult *Anguillicola crassus* were counted and dried at 50°C to determine dry weight.

In order to quantify infection with *Ichthyophthirius multifiliis*, the number of trophozoites cm^{-2} eel skin were counted under a binocular microscope immediately after swimming ended. We also examined the eels' gills for *I. multifiliis*, but since they were less densely infected than the skin, we did not count the number of trophozoites.

Statistical analysis. According to the abundance and dry weight of the *Anguillicola crassus* they bore, eels were divided into 4 classes (I: uninfected; II: 1 to 5 nematodes, 0.1 to 1.0 mg dry wt; III: 6 to 10 nematodes, 1.1 to 25.0 mg dry wt; IV: >10 nematodes, ≥25.1 mg dry wt). A condition factor was calculated from the length and weight of eels as described by Schäperclaus (1990). Data on the swimming activity of each group are presented as means ± SD. A Kruskal-Wallis *H*-test or Mann-Whitney *U*-test was employed to test for

Table 1. *Anguilla anguilla*. Swimming duration ($\bar{x}$ ± SD) in relation to dry weight of *Anguillicola crassus*

Dry wt of *A. crassus* (mg)	No. of eels	Duration (s)
Uninfected	14	141 ± 110
0.1–1.0	16	169 ± 137
1.1–25.0	19	136 ± 85
≥ 25.1	21	197 ± 168

Table 2. *Anguilla anguilla*. Swimming duration ($\bar{x}$ ± SD) in relation to number of *Anguillicola crassus* swimbladder^{-1}

No. of *A. crassus*	No. of eels	Duration (s)
0	14	141 ± 110
1–5	37	177 ± 131
6–10	8	149 ± 119
>10	11	192 ± 181

significant differences ($p \leq 0.05$). Spearman's rank-correlation coefficient was used to test for significant associations between swimming activity and the infection status.

RESULTS

Swimming activity of eels infected with *Anguillicola crassus*

Eels could be grouped into 4 classes based on the dry weight of the nematodes in their swimbladders (Table 1). The duration of swimming activity did not differ significantly between these groups. However, eels with the highest dry weight of nematodes (>25.1 mg) tended to swim longest.

Similar results were obtained when eels were grouped according to the number of adult worms per swimmbladder (Table 2). Eels with 10 or more nematodes seem to swim longer against the current than less infected hosts, but again the differences were not significant. Spearman's rank-correlation analysis did not show any association between the degree of infection with *Anguillicola crassus* (dry weight and number) and swimming activity (Fig. 2). Furthermore, swimming activity was not correlated with the condition factor of the eels (Spearman r = 0.102; p = 0.05).

Swimming activity prior to and after infection with *Ichthyophthirius multifiliis*

In contrast to *Anguillicola crassus* infection, infection of eels with *Ichthyophthirius multifiliis* significantly reduced the duration of active swimming against the current (Fig. 3). By 4 d post-exposure, 58 of 70 eels (83%) had become infected with *I. multifiliis*. On these eels (39 of which were used for the experiments) the protozoan abundance averaged 30.7 ± 17 trophozoites cm^{-2}. Prior to infection, the eels swam against the current for 157 ± 109 s. This decreased to 83 ± 53 s after infection with the ciliate (Fig. 3).

DISCUSSION

In the present study, the swimbladder nematode *Anguillicola crassus* was found in 88.5% of the eels, a level comparable with that found in other aquatic biotopes in Europe. Sures & Streit (2001) reported a prevalence of approximately 90% for the river Rhine near Karlsruhe. Our results from the swimming channel indicate that *A. crassus* does not affect the swimming ability of infected eels in terms of the maximum period of time the eels are able to withstand a current of 0.62 m s^{-1}. This corresponds to findings of

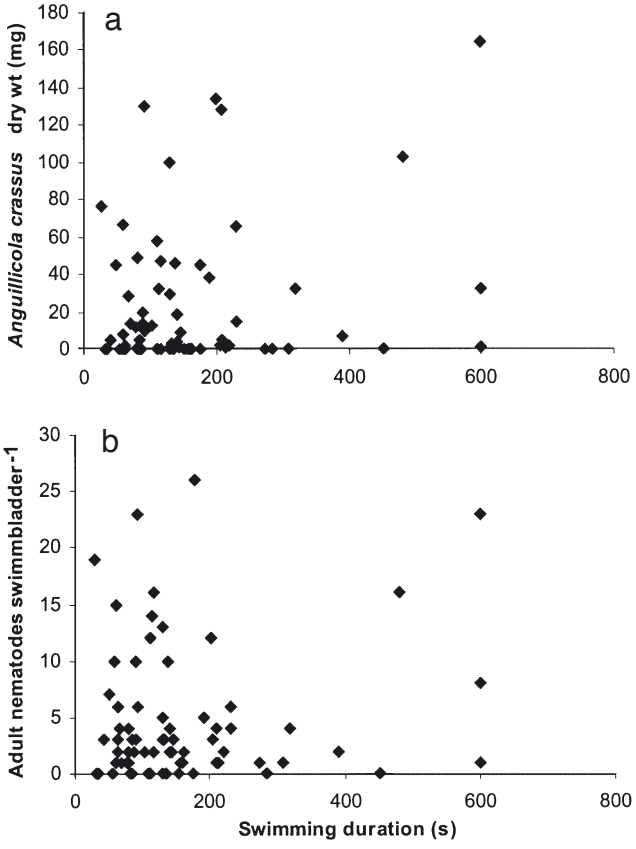

Fig. 2. *Anguilla anguilla*. Swimming duration in relation to (a) dry weight of *Anguillicola crassus* and (b) numbers of *A. crassus* eel^{-1}

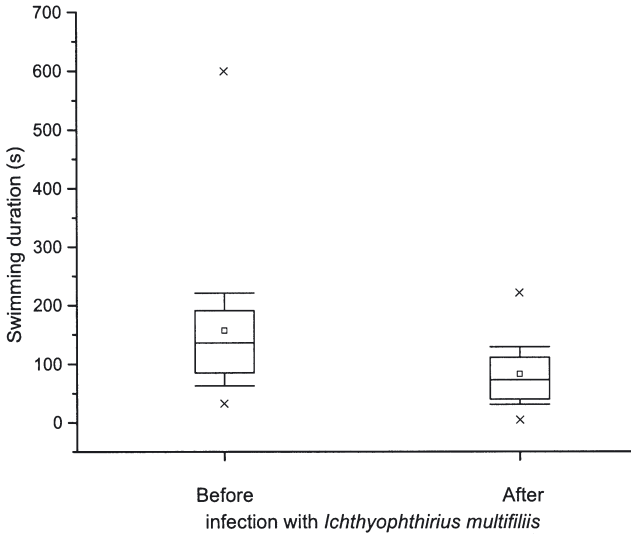

Fig. 3. *Ichthyophthirius multifiliis*. Swimming activity before and after infection with *Ichthyophthirius multifiliis*. All measured values are shown: ×: maximum/minimum; □: arithmetic mean; horizontal line at top, inside and at bottom of box: 25th, 50th, and 75th percentile values respectively. Error bars: 5th and 95th percentiles

Nimeth et al. (2000), who also did not detect any significant difference in swimming activity between uninfected and *A. crassus*-infected glass eels. They measured the 'critical' swimming speed (defined as the speed at which the glass eels were no longer able to swim against the current), and found that at intermediate speeds (~60 to 80% of the critical swimming speed) infected fish had a slightly higher locomotion than uninfected control eels.

In contrast to our results and those of Nimeth et al. (2000), Sprengel & Lüchtenberg (1991) reported an effect of parasites on the swimming performances of eels. They measured the maximum swimming speed of European eels *Anguilla anguilla* in a circular channel to determine their fitness, and reported reductions in maximum swimming speed in direct parallel to increasing numbers of *A. crassus*. In heavily infected eels (≥11 nematodes), swimming ability was reduced by 18.6% compared to uninfected fish.

We do not know the circumstances under which the apparently conflicting results of Sprengel & Lüchtenberg (1991) were achieved. The present study comprised parallel experiments using a reference host-parasite model, an approach that proved useful in detecting different effects of various parasites on the locomotion of a host.

Ichthyophthirius multifiliis, a parasite which quickly multiplies on an individual host, considerably affected the swimming behaviour of infected eels. The eels displayed dramatically reduced swimming activity after infection with this parasitic protozoan. Statistically significant differences between swimming activity before and after infection with *I. multifiliis* were revealed by a Mann-Whitney *U*-test. Infected eels swam against the current for >1 min less than prior to infection. Thus, their swimming ability was reduced by 47%. In 4 cases, the eels completely lost the ability to withstand the current and they drifted passively into the net at the end of the tube. We interpret this as a clear pathological effect of infection rather than an adaptive behavioural alteration, as this monoxenic parasite would not profit from exposing infected fish to predation reducing their swimming ability. *I. multifiliis* is well known to have severe pathogenic effects on both the skin and the gill of eels (Ewing & Kocan 1987, Ewing et al. 1988), causing for instance a lower rate of respiration and thus a loss of fitness, leading to death in fish that are heavily infected.

With regard to *Anguillicola crassus*, the eel is its final host, and thus an altered locomotary behaviour which increases vulnerability to predation would not be profitable either. According to our results and those of Nimeth et al. (2000), infected eels were even slightly better in swimming against a water current than uninfected controls. This suggests that *A. crassus* infection is associated with an increased short-term energy availability channelled by the endocrine system. Sures et al. (2001) showed that infection with L_3-larvae of *A. crassus* resulted in a significant increase in the serum cortisol levels of infected eels. Obviously, the larvae invading the swimbladder wall induce stress in European eels and thus lead to elevated levels of cortisol, which could increase the concentration of plasma carbohydrates providing energy. Cortisol is generally considered a primary messenger of a stress response in teleostean fishes (Barton & Iwama 1991, Kloas 1999). This might explain the better swimming efficiency in our short-time experiments. However, this should not function in the long-term, and in the experiments by Sures et al. (2001) no elevated cortisol levels were found in eels with mature *A. crassus*. It should be noted that in the experiments of Sures et al. (2001) the infected eels had not been stressed in any way.

The probability of an eel reaching the spawning grounds in the Sargasso Sea and the speed at which this long-distance migration can be performed will depend on the energy reserves and overall condition of the eel. One of the most important energy reserves is the liver (Wootton 1984, Lambert & Dutil 1997). The major energy reserve of the eel consists of lipids, which are predominantly stored as triglycerides in muscle tissues (Lewander et al. 1974, Boëtius & Boëtius 1980) and in the liver (Dave et al. 1975). However, analogous to the results of our swimming experiments, Möller et al. (1991) found no indication of the liver somatic index

of *Anguilla anguilla* being influenced by *A. crassus*, and therefore also no effect on the energy reserves of the host.

In our study the short-term ability to resist a water current was not correlated with the condition of the eels. In nature, the smaller male silver eels start their spawning migration in European inland waters earlier (August, September) than the larger, heavier females (September, October) because they do not attain a swimming speed of more than ~40 km d^{-1}. By March, both sexes have arrived at the spawning grounds, and mating commences (Tesch 1999). Inside rivers, silver eels use the currents (especially after heavy rain) for passive displacement towards the sea, where they can float out on the low-tide current. In the open Atlantic, migration takes place at depths mostly below 100 m, where currents do not play a major role. However, eels perform diurnal, vertical, lunar-controlled migrations. On dark nights, migration takes place at depths between ~40 and 250 m, during the day between 300 and 500 m. For such vertical migrations, an uninfected swimbladder, with unaltered stratification and superficially located, intact gas gland cells would seem to be an essential requirement. Infection by *Anguillicola crassus* leads to thickening and disorganization of the swimbladder wall, with the superficial gas gland cells losing direct contact to the blood capillaries (Würtz & Taraschewski 1996). In such swimbladders, oxygen content is decreased, suggesting that the function of this hydrostatic organ is disturbed. Eels with pathologically altered swimbladders may have difficulty in performing vertical migrations, and thus may use up too much of their energy reserves, resulting in a reduced swimming speed and thus a late arrival at the spawning grounds.

In a normal vertebrate mating system individuals of the choosing (usually the female) sex select the fittest mates from a group of several others (Gould & Gould 1989). In European eels, mating and spawning takes place at a depth of several hundred metres (Tesch 1999), where sexual selection cannot rely on optical cues such as size of pectoral fins, colourful breast, or other mating ornaments reflecting the status of health (Gould & Gould 1989). Under these circumstances it would be selectively profitable to exclude individuals that arrive late at the spawning ground from reproduction. From an evolutionary viewpoint, *Anguilla anguilla* would benefit most if 'good genes' which have prevented certain eels from becoming infected could be passed on to offspring, while infected eels serve as reserve mates. Infected late arrivals would comprise both sexes; thus, the earlier arrivals should be present in a balanced male:female ratio, enabling successful reproduction. Eels with a thickened, fibrotic swimbladder wall may be subjected to higher predatory pressure during their slower, vertical migrations, or may suffer high mortality due to other adverse factors. Therefore, the overall reproductive output of the European eel under the impact of *Anguillicola crassus* is possibly slightly lower than it was before the parasite occurred in Europe, but the selection of 'good genes' is ensured.

It does not seem likely that the decrease in the number of glass eels arriving at the coasts of Western Europe is predominantly caused by *Anguillicola crassus* preventing silver eels from reaching the Sargasso Sea. Intensive aquacultures rearing European eels in Europe and in China, and various other ecological alterations, such as canalization or the destruction of river systems by power stations, could be more important factors. Also, the decrease in the abundance of glass eels had already begun prior to the spread of *A. crassus* in Europe (Würtz & Taraschewski 2000). Accordingly, infection of eels with *A. crassus* is probably only 1 (minor?) factor among an array of threats to the European eel.

Acknowledgements. Thanks are due to Professor H. Buggisch and Professor C. Posten (Institut für Mechanische Verfahrenstechnik und Mechanik) for permitting the use of the swimming channel. The expert repair and assistance of their technical employees in running the swimming channel is gratefully acknowledged. Thanks are also due to Mr. H. Weiher (Institut für Wasserwirtschaft und Kulturtechnik) for lending a flow-meter.

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Editorial responsibility: Wolfgang Körting, Hannover, Germany

Submitted: October 28, 2003; Accepted: February 19, 2004
Proofs received from author(s): July 30, 2004