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# Swimming performance of silver eels is severely impaired by the swim-bladder parasite *Anguillicola crassus*

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**Abstract**

Infection with the swim-bladder parasite *Anguillicola crassus* is suggested as one of the principal causes of the collapse of the European eel population. This nematode has been introduced in Europe from Asia in the 80s and parasitized in a short time *Anguilla* eel species in different geographical regions across the globe. The parasites drain energy due to their sanguivorous feeding and they cause mechanical damage on the swim-bladder wall. These two effects are hypothesized to impair the spawning migration of the European eel. In this study, we have investigated both effects on swimming performance. We hypothesized that parasitic sanguivorous activities – related to parasite weight – reduce swimming endurance, while mechanical damage of the swim-bladder impairs buoyancy control. Eighty eels suffering various degrees of infection were introduced in swim-tunnels and subjected to a swimming fitness test. The relation between *A. crassus* infection and swimming efficiency was measured for large female silver eels swimming at various speeds. Infected eels had lower cruising speeds and a higher cost of transport. Eels without parasites, but with a damaged swim-bladder showed similar effects. Almost half of the eels that contained damaged swim-bladders (43%) stopped swimming at low aerobic swimming speeds (<0.7 m/s). Simulated migration trials in a recent related study have confirmed that eels with a high parasite level or with damaged swim-bladder show early migration failure (<1000-km). Reduced swimming performance appears to be associated with swim-bladder dysfunction. As we found that especially silver eels have much higher infection levels than yellow eels, it is concluded that migrating silver eels with severely infected or damaged swim-bladders are unable to reach the spawning grounds.


*Keywords:* *Anguillicola crassus* (Kuwahara, Niimi and Hagaki, 1974); Environmental constraint; European eel *Anguilla anguilla* (Linnaeus 1758); Oxygen consumption; Reproductive migration; Swimming efficiency; Swimming endurance

## 1. Introduction

Eel populations world-wide are dangerously close to collapse (Anonymous, 2003). A steep decline started in the 80s and ever since no signs of recovery have been observed. Several causes have been suggested such as global change, over fishing, habitat destruction, pollution and introduction of new diseases. Between 20 and

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30 years ago two new diseases were introduced from Asia to Europe and the Americas, *e.g.* a virus EVEX (van Ginneken et al., 2004, 2005a) and a nematode infection with *Anguillicola crassus*. The latter was not endemic but originally a parasite of the Japanese eel *Anguilla japonica.* It took about one decade to spread the *A. crassus* infection over large parts of Europe (Neumann, 1985; Székely et al., 1991; Moravec, 1992; Evans and Matthews, 1999) and more recently it has reached North America (Johnson et al., 1995). In a short time, various eel species across the globe became parasitized (Moravec and Taraschewski, 1988), due to world-wide eel shipments (reviewed by Taraschewski, 2006).

Since its introduction in Europe around 1982, many authors described the life cycle of *A. crassus* (Haenen et al., 1989; De Charleroy et al., 1990; Thomas, 1993). Clearly the European eel is more sensitive and less effective in its defence against *A. crassus* than the Japanese eel (Egusa, 1979; van Banning and Haenen, 1990; De Charleroy et al., 1990; Boon et al., 1990a, Molnár et al., 1991; Molnár et al., 1993; Knopf and Mahnke, 2004), which is typical for infection with a non indigenous parasite.

There are two kinds of adverse effects of *A. crassus* infection (Höglund et al., 1992) on the host: 1) energy drain due to sanguivorous activities of the parasite, and 2) mechanical damage of the swim-bladder wall. Concerning the first effect, Boon et al. (1990b) found that the sanguivorous activities of the parasites decrease the number of circulating erythrocytes and therefore the $O_2$ carrying capacity. Severely infected eels are therefore presumed to have lower aerobic performance. Molnár (1993) proved that by decreasing the $O_2$ content of the water severely infected eels die first, while uninfected specimens endure the hypoxic condition for a long time. The second effect, i.e. severe damage to the swim-bladder wall, is caused by migratory activity of the larvae in the swim-bladder wall, and the direct invasion of the pre-adults and adults in blood vessels result in extensive damage of the bladder wall (Molnár et al., 1993). Pathological changes include haemorrhages, formation of parasitic nodules, inflammatory cell proliferation, and hypertrophy of connective tissue, necrotic areas and oedema. These changes eventually cause a substantial thickening of the swim-bladder wall (Molnár et al., 1993; Beregi et al., 1998) and a major reduction of the swim-bladder volume. A severely damaged swim-bladder cannot control the buoyancy of the animal, a crucial function for fishes in open water.

Effects of severe *A. crassus* infection are thought to impair the migration to the spawning grounds in the Sargasso Sea and therefore also to impair reproduction. Since eels migrate about 5500-km, probably at great depths, a decrease of the $O_2$ carrying capacity of the blood combined with a disabled swim-bladder will likely reduce the swimming capacity. Parasitism does not seem to impede pressure resistance (Vettier et al., 2003). However, the eels in the high pressure experiments stayed on the bottom of the tank, so those experiments did not provide conclusive evidence for a functional swim-bladder. Two earlier studies investigated the influence of *A. crassus* on eel swimming performance (Sprengel and Lüchtenberg 1991; Münderle et al., 2004). However, those studies were carried out on small yellow eels ($\leq$45 cm). Obviously, large silver eels should be tested over long distances and periods, as not only swimming speed but particularly a low cost of transport and a high endurance are crucial for long distance migration.

Recently, we developed an experimental test to quantify swimming performance (Palstra et al., 2006a) using 22 swim-tunnels suitable for exercising many large female silver eels at the same time. This test and set-up was used to investigate the relation between swimming endurance and the adverse effects of *A. crassus* infection.

## 2. Materials and methods

### 2.1. Choice of experimental eels

We used eels from Lake Balaton for two reasons. First, the population of Lake Balaton eels generally displays high infection levels, especially at the end of the summer (Molnár et al., 1991, 1993). Second, Lake Balaton eels were at the time of the experiments at least 12 years old, since the lake was restocked with glass eels in spring 1991 for the last time and has no endemic eel population (Bíró, 1992). Older eels are more likely to change into the migratory (silver) state by the end of the summer.

### 2.2. Catch, selection and X-ray of experimental eels

At the end of August of 2002 and 2003, 40 eels were caught each year by electro-fishing in Lake Balaton (Hungary) in the region of Keszthely and Tihany. Eels were transported to the laboratory in $O_2$-filled plastic bags and kept in concrete basins or plastic tanks with flow-through water until they were scanned by means of X-ray (Fig. 1) using the method described by Beregi et al. (1998) and Székely et al. (2005). X-ray scans were used to measure the swim-bladder length (SBL) and to

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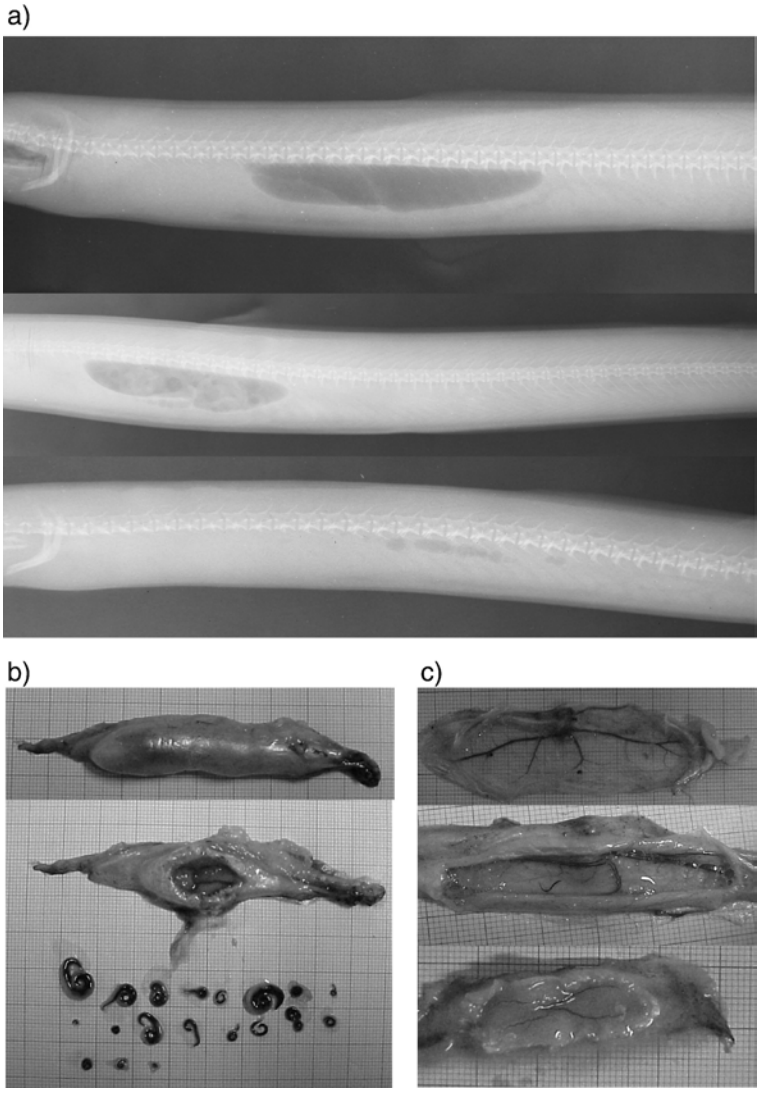


Fig. 1. Variation in infection level is illustrated by X-ray with a) an eel with a large, uninfected bladder (top), an eel with a medium-sized bladder with visible parasites (middle) and an eel with a small bladder with minimal volume (bottom), b) Dissection of the swim-bladder, whole (top) and cut open (bottom) showing 19 parasites of various sizes and c) three levels of swim-bladder wall transparency, -thickness and length showing a large, thin-walled transparent swim-bladder (top), a medium-sized swim-bladder with a thicker wall (middle) and a small thick-walled non-transparent swim-bladder (bottom).

determine the actual swim-bladder status. Eels were marked individually by injecting "Passive Integral Transponder" (PIT)-tags (TROVAN) subcutaneously just behind the head. After a few days' rest, the eels were packed into large $O_2$-inflated nylon bags in boxes and sent to Leiden by air-mail early September (2002 and 2003).

### 2.3. Swim-tunnel set-up and $O_2$ consumption

A set of 22 Blazka-type 127-l swim-tunnels as described by van den Thillart et al. (2004) were used for the swimming trials. The tunnels are placed in the direction of the Sargasso Sea (WSW) in a climatized room of about 100-$m^2$. A total water content of about 7000-l was recirculated continuously over a bio-filter. The illumination in the climatized room was switched to 670-nm light (bandwidth 20-nm). Based on pigment changes during silvering, it is assumed that this far-red light is invisible for eels (Pankhurst and Lythgoe, 1983). The $O_2$ level in each tunnel was measured continuously by an $O_2$ electrode (Mettler Toledo). The $O_2$ consumption rate was calculated from the $O_2$ decline after automatic closure of the water-inlet by a magnetic valve.

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From the decline of the $O_2$-concentration, the $O_2$ consumption rate was calculated following the formula:

$$\dot{M}O_2 = (127^{*}\Delta[O_2]/\Delta t)/\mathrm{BW}(\mathrm{mg}O_2/\mathrm{kg\ eel/h}),$$

where $(127 * \Delta[O_2]/\Delta t)$ is the decrease of the $O_2$ content in the swim-tunnel of 127-l per hour and BW is body weight.

### 2.4. Experimental protocol

Experiments were performed in 2002 and 2003. In each year 40 eels were introduced into the swim-tunnels, running with fresh water of 18±1 °C, at least two days before the experiment started. Prior to introduction eels were anaesthetized with clove oil (1:10 dissolved in 100% ethanol using a dosage of 1–1.5 ml per l water). $O_2$ electrodes were calibrated with sodium sulphite and air.

Before swimming, the $O_2$ consumption of all resting eels was measured for a period of 3–4 h. Eels were subjected to a swimming fitness test described in Palstra et al. (2006a). Briefly, eels started to swim at a swimming speed ($U$) of 0.5 m/s for 2 h. During these 2 h, the $O_2$ decline was measured over the first 1.5 h. Thereafter the tunnel was flushed for 0.5 h. The speed was raised by 0.1 m/s to 0.6 m/s for 2 h; also during the first 1.5 h the $O_2$ decline was measured. The same procedure was repeated with steps of 0.1 m/s raising the $U$ up to 1.0 m/s. In case the $O_2$ levels fell below 75% air saturation (AS), flushing occurred automatically, raising the AS level within 15 min to 85%. The swimming behaviour of the eels and their position in the swim-tunnel was registered every 15 min. When the fish fatigued during the trials, the velocity was lowered immediately to 0.1 m/s. This velocity can be considered as the resting state as the eels stayed most of the time at the bottom.

### 2.5. Swimming parameters

Five parameters were used to characterise swimming capacity and efficiency (Palstra et al., 2006a):

1) $\dot{M}O_{2\ \mathrm{rest}}$: $O_2$ consumption at rest in mg $O_2$/kg/h,
2) $\dot{M}O_{2\ \mathrm{max}}$: $O_2$ consumption at max endurance in mg $O_2$/kg/h,
3) $U_{\mathrm{crit}}$: The critical aerobic swimming speed (m/s) calculated according to Brett (1964),
4) $U_{\mathrm{opt}}$: The optimum swimming speed in m/s. Speed at which energy spend per distance (mg $O_2$/kg/km) reaches a minimum (Tucker, 1970),
5) $\mathrm{COT}_{\mathrm{min}}$: The cost of transport at $U_{\mathrm{opt}}$ in mg $O_2$/kg/km.

The $U_{\mathrm{opt}}$ was determined by plotting a polynomial trend line through COT values vs. swimming speeds per individual eel. The point on this trend line with the lowest COT ($\mathrm{COT}_{\mathrm{min}}$) was calculated by setting the first derative to zero.

### 2.6. Measurements and sampling

Morphometric parameters: body length (BL, cm), body weight (BW, g), swim-bladder length (cm), eye diameter horizontal (EDh, mm) and vertical (EDv, mm), pectoral fin length (PFL, cm) were used to calculate:

- Fulton's condition factor $K = 100 * \mathrm{BW}/\mathrm{BL}^3$
- Eye index (Pankhurst, 1982) $\mathrm{EI} = 100 * ((\mathrm{EDh} + \mathrm{EDv})/4)^2\pi/10 * \mathrm{BL})$
- Pectoral fin index (Durif et al., 2005) $\mathrm{PFI} = 100 * \mathrm{PF}/\mathrm{BL}$
- Silver index (Durif et al., 2005) SI = function of (BL, BW, ED and PF)

For the determination of the infection level:

- Parasite index $\mathrm{PI} = (\mathrm{PW}/\mathrm{BW})$

Where PW is the parasite total weight (mg) and BW is the eel body weight (kg).

For determination of mechanical damage:

- Swim-bladder index $\mathrm{SBI} = (\mathrm{SBL}/\mathrm{BL})$

Where SBL is the swim-bladder length (cm) and BL is the eel body length (cm).

From the eels of 2003, 0.5 ml blood was taken before and after swimming. Haemotocrit (Hct) was determined immediately upon sampling. The remaining blood was centrifuged for 5 min at 14,000 rpm and blood plasma was stored at −80 °C for later analysis of total blood protein (TP). Pre- and post-swimming blood plasma was defrosted on ice, 30 times diluted and measured for TP content with a bicinchoninic acid protein assay (assay #23225, Pierce Chemical Company, USA). The swim-bladder was dissected, photographed on a reference mm grid and the number of parasites was determined (Fig. 1). Parasites were preserved in 4% buffered formalin. These samples were used for wet weight determination of parasites (PW).

### 2.7. Statistics

Normality of data distribution was tested with Kolmogorov–Smirnov tests. For comparison of parameters before and after swimming, one-tailed paired $t$-tests were performed. For comparison between good

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and bad swimmers and between eels of various silver stages, one-tailed unpaired *t*-tests were performed. For comparison of eels with healthy, infected and damaged swim-bladders, a one-tailed univariate analysis of covariance (ANCOVA) was performed. Body length or body weight was used as cofactor. In case the cofactor did not have a significant influence and to estimate between which groups the effect was significant, ANOVA with post-hoc Bonferoni correction was performed. Comparison between the eels that finished the swimming trials and the "drop-outs" was tested with a Mann–Whitney *U* test. For correlation analyses, one-tailed Pearson tests were performed. All tests were performed with SPSS 10.0 for Windows. Results were calculated and plotted as means ± standard error (SE).

## 3. Results

### 3.1. Status of eels before swimming

The experimental eels ($n=80$) measured 67 ± 1 cm (range 54–82 cm), weighed 466 ± 16 g (range 228–865 g), and had a condition factor K of 0.15 (Table 1a). The mean eye index (EI) was 8.38 ± 0.28. As 71% of the eels had EI > 6.5 the majority could thus be considered as silver (Pankhurst, 1982). This was confirmed by the high silver index of 3.9. Among the experimental eels 4% were in stage FII (residents), 56% in stage FIII (pre-migrants) and 40% in stage FV (active migrants); no eels were in stage FIV. The pectoral fin index (PFI) showed little variation between (yellow and silver) eels and was 4.80 ± 0.05%. When considering characteristics of eels in the various migratory stages, stage FII residents ($n=3$) were the smallest at 57 ± 1 cm weighing 279 ± 7 g with a K of 0.15. Stage FIII pre-migrants ($n=39$) were larger and measured 64 ± 1 cm, weighing 390 ± 16 g with a K of 0.15. Stage FV migrants ($n=35$) were the largest measuring 71 ± 1 cm, weighing 573 ± 21 g with a K of 0.16.

Table 1
Parameters of experimental eels (mean ± SE and range) with a) morphometric parameters of experimental eels (BL = body length, BW = body weight, *K* = condition factor, EI = eye index, PFI = pectoral fin index, SI = silver stage), b) parasite parameters; swim-bladder damage was estimated by its length (SBL) and was determined by X-ray. Infection level was given by the number of parasites and parasite weight (PW) and was determined by dissection and c) blood parameters before (pre) and after (post) swimming

| | | | *n* | Mean | SE | Range |
|---|---|---|---|---|---|---|
| a) Parameter | BL | (cm) | 80 | 67 | 1 | 54–82 |
| | BW | (g) | 80 | 466 | 16 | 228–865 |
| | K | | 80 | 0.15 | 0.00 | 0.11–0.20 |
| | EI | | 80 | 8.38 | 0.28 | 4.99–16.34 |
| | PFI | | 80 | 4.80 | 0.05 | 3.80–6.05 |
| | SI | | 80 | 3.9 | 0.1 | 2, 3, 5 |
| b) Damage | SBL | (cm) | 78 | 7.22 | 0.28 | 2.1–12.0 |
| | SBI | (%) | 78 | 10.8 | 0.4 | 3.0–19.0 |
| Infection | Parasites | (n) | 78 | 3.4 | 0.6 | 0–28.0 |
| | PW | (mg) | 71 | 150 | 30 | 0–1930 |
| | PI | (mg/kg) | 71 | 299 | 61 | 0–2950 |
| c) Pre-swimming | Hct | (%) | 40 | 31.4 | 1.2 | 10.2–48.4 |
| | TP | (mg/ml) | 40 | 52.8 | 0.9 | 38.3–64.6 |
| Post-swimming | Hct | (%) | 40 | 32.8 | 0.9 | 20.6–44.4 |
| | TP | (mg/ml) | 40 | 53.5 | 0.7 | 46.9–64.3 |

Paired observations on eels from the 2003 experiment ($n=40$) of Hct and TP are shown.

### 3.2. A. crassus infection and swim-bladder damage

The swim-bladder length (SBL) as indicator of shrinkage due to inflicted damage was non-invasively determined on 78 eels by X-ray before swimming (Fig. 1a); two eels were not scanned. The SBL was 7.22 ± 0.28 cm (range 2.1–12.0 cm; Table 1b). Relatively to the length of the eel (swim-bladder index SBI) these values were 10.8 ± 0.4%. After swimming, swim-bladders were dissected. The numbers of parasites were between 0 and 28 (Fig. 1b; Table 1b). Parasite weight (PW) was between 0 and 1930 mg; relative to the weight of the eel (parasite index PI) these values were 299 ± 61 mg/kg. We observed that the SBL was correlated to its volume, transparency, and thickness of the wall (Fig. 1c). Eels had swim-bladders with SBIs in the range 5.0–15.6 with a median of 10.3% (Fig. 2). The median SBI was used to discriminate small and large swim-bladders. Swim-bladders with SBI < median 10.3% contained 25% of the accumulative parasite weight while those with SBI > median 10.3% contained 75% of the accumulative parasite weight. Thus, larger swim-bladders exhibited higher parasite levels. On the other hand, when the swim-bladder was small, the parasite level was also small. Non-infected swim-bladders of all sizes could be found. Large swim-bladders had thin, semi-transparent walls and showed only slight signs of damage (thickening) or pre-infection. The smallest swim-bladders had always damaged and thickened walls. The latter condition results from previous infections and makes the swim-bladder less suitable for re-infection (Lefebvre and Crivelli, 2004).

We pooled data into three groups based on the presence of parasites (infected/not infected) and on level of swim-bladder damage (long vs. short swim-bladder):

1. Infected eels ($n=43$); a group with swim-bladders of variable length and wall thickness.

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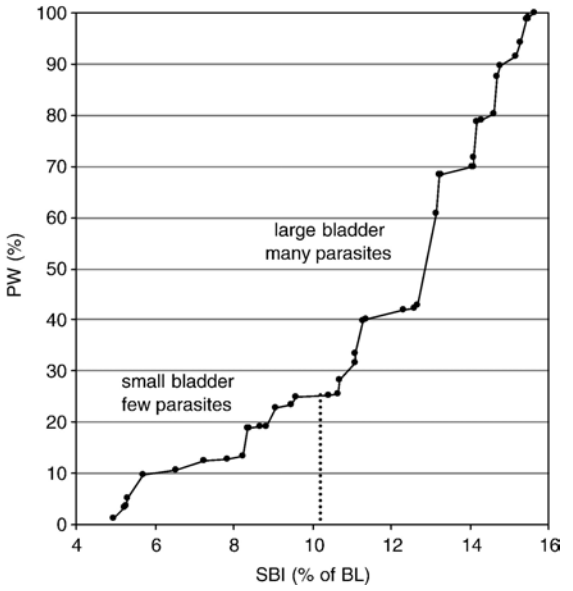


Fig. 2. Accumulative parasite weight PW (%) plot against the swim-bladder index SBI (% of BL) of infected eels. Indicated by the dashed line is the median SBI which was used to discriminate between small and large swim-bladders. The smaller swim-bladders have lower parasite levels and contain 25% of the accumulative PW, while larger swim-bladders exhibit higher levels and contain 75% of the accumulative PW.

2. Non-infected eels ($n=27$);
   a. Healthy Eels with large (empty) swim-bladder ($n=13$); a healthy group with large, thin-walled swim-bladders (SBI $\geq$ 10.3%) and without parasites
   b. Eels with damaged swim-bladders ($n=14$); a group with damaged small swim-bladders (SBI $<$ 10.3%) and without parasites.

### 3.3. Relation between silver stage, parasite weight and swim-bladder length

Parasite index (PI, derived from parasite weight) and swim-bladder index (SBI, derived from swim-bladder length) were compared between eels of different silver stages. A clear correlation existed between the silver stage and the PI (Fig. 3). The parasite index significantly increased with progression of the silver stage; a significant difference was observed between stage FII and stage FIII ($P<0.001$), as well as between stage FIII and the active migrants stage FV ($P<0.05$). A similar effect was however not observed with respect to swim-bladder damage.

### 3.4. Swimming of experimental eels

A complete set of swimming data was collected on 74 eels. In general, two groups of swimming eels could

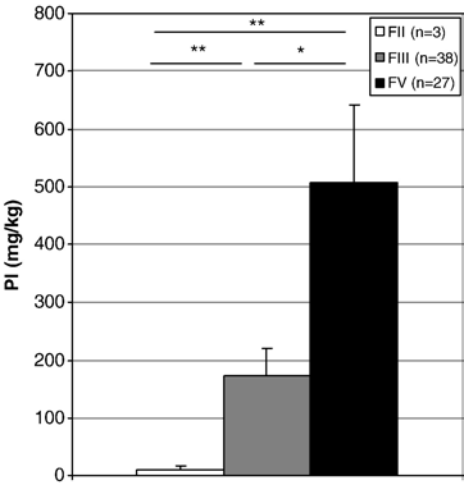


Fig. 3. Relative parasite weight (PI in mg/kg) in experimental eels representing silver stage FII, FIII and FV. Stage FIV was not represented. Active migrant silver eels harbored significantly more parasites and had a higher PI (*$P<0.05$ and **$P<0.001$) than residents and pre-migrants.

be distinguished. A group of eels (referred to as "drop-outs", $n=27$) stopped swimming before reaching a swimming speed of 0.7 m/s. These eels swam unsteadily and were unable to maintain their balance in the swim-tunnel. The number of data points did not suffice to derive the polynomial curve and thus to determine the optimum swimming speed ($U_{opt}$) and cost of transport

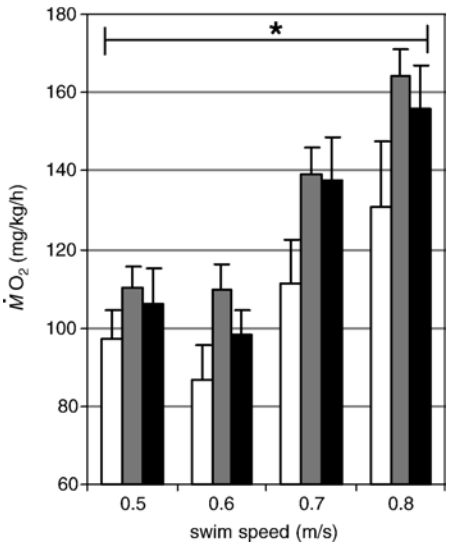


Fig. 4. $O_2$ consumption levels ($\dot{M}O_2$) of healthy eels (white bars), infected eels (grey bars) and eels with damaged swim-bladders (black bars) at swimming speeds between 0.5 and 0.8 m/s. $\dot{M}O_2$ was higher (ANCOVA; $P<0.01$) for infected eels and eels with damaged swim-bladders on basis of pooled swimming speed data.

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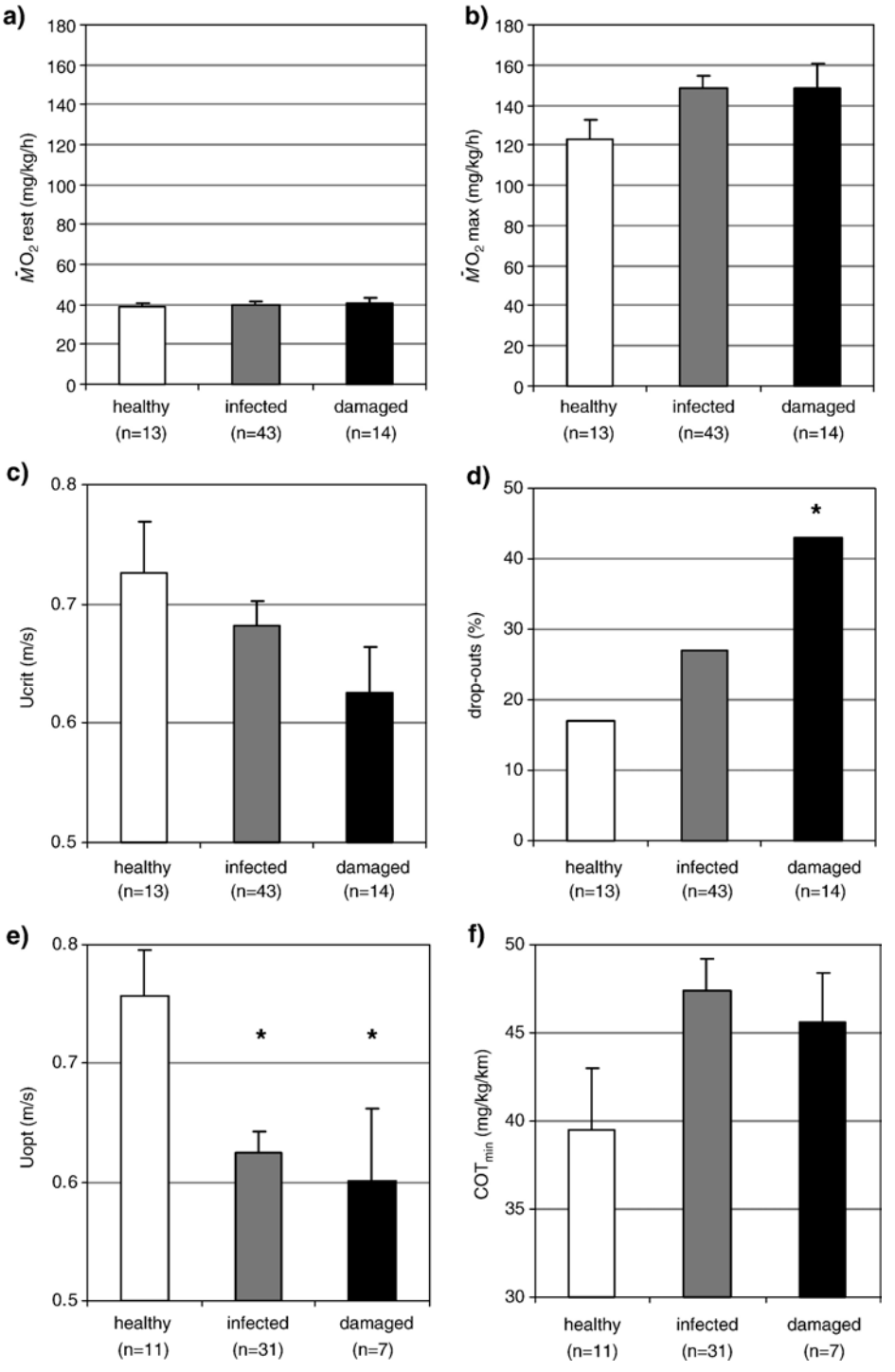


Fig. 5. Swimming parameters of healthy eels (white bars), infected eels (grey bars) and eels with damaged swim-bladders (black bars). Healthy eels had large swim-bladders (SBI ≥ 10) without parasites. Infected eels had all-sized swim-bladders with parasites. Eels with damaged swim-bladders had small swim-bladders (SBI < median 10.3%) without parasites. Significant differences ($P<0.05$) are indicated by asterisk. No significant differences were found for a) $O_2$ consumption in rest ($\dot{M}O_{2\ rest}$) b) and maximal $O_2$ consumption ($\dot{M}O_{2\ max}$), c) critical swimming speeds ($U_{crit}$) tended to decrease with increasing damage and d) 43% of these eels dropped out before reaching $U_{opt}$ (Mann–Whitney; $P=0.03$), e) eels with small swim-bladders had lower optimum swimming speeds $U_{opt}$ (ANCOVA; $P=0.01$) and f) cost of transport ($COT_{min}$) tended to increase with increasing damage.

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($COT_{min}$) for these eels. The other group consisted of steady swimmers (referred to as "swimmers", $n=47$). They continued at swimming speeds ≥0.7 m/s, and from this group we could measure all swimming parameters. The drop-outs had lower PI and SBI values although not significantly different. The drop-outs had a critical swimming speed ($U_{crit}$) of 0.54±0.01 m/s vs. a $U_{crit}$ of 0.73±0.01 m/s for the swimmers. The $\dot{M}O_2$ rates of the drop-outs were significantly higher. At rest, the difference between drop-outs and swimmers was not significant (respectively 41.7±2.1 vs. 38.4±1.2 mg/kg/h), but already at the start of the swimming trial (at 0.5 m/s) the difference was significant ($P<0.05$), 129±10 vs. 101±9 mg/kg/h for the drop-outs and the swimmers, respectively. The drop-outs had lower haematocrit ($P=0.07$), 29.3±1.2 vs. 33.1±1.3% for the swimmers.

### 3.5. Influence of infection and damage on swimming performance

To analyse the influence of infection and damage on swimming, we compared values of swimming parameters between the healthy, the infected and the damaged group by ANCOVA. Fig. 4 shows $O_2$ consumption ($\dot{M}O_2$) levels at the various swimming speeds. $\dot{M}O_2$ levels ($P=0.01$) were significantly higher in the infected (13%) as well in the damaged groups (9%) at all swimming speeds.

No difference was found in $O_2$ consumption at rest ($\dot{M}O_{2rest}$; Fig. 5a) between the different groups. Maximum $O_2$ consumption ($\dot{M}O_{2max}$; Fig. 5b) was higher in infected and eels with damaged swim-bladders but not significantly. Critical swimming speed ($U_{crit}$) was lower in the infected group and even more in the damaged group (Fig. 5c) but also not significantly different. In the healthy group of eels, the percentage of drop-outs was 17% (Fig. 5d). In the infected group of eels, this percentage was higher (27%). Of the eels with damaged swim-bladders, 43% dropped out which was significantly different ($P<0.05$) from the healthy eels (Fig. 5d).

The optimum swimming speed ($U_{opt}$) was 18 and 21% lower ($P=0.01$) in respectively infected eels and eels with damaged swim-bladders (Fig. 5e). Healthy eels had $COT_{min}$ values of 40 mg/kg/h, the values of eels with damaged swim-bladders and infected eels were higher (not significantly) by respectively 18 and 21% (Fig. 5f). Fig. 6 shows $\dot{M}O_2$ and $COT_{min}$ levels of three typical examples: a healthy eel (PI=0, SBI=12.7), an infected eel (PI=2950, SBI=13.1) and a damaged eel (PI=0, SBI=3.0). The healthy eel had the lowest $\dot{M}O_2$ and by far the lowest COT values.

### 3.6. Blood parameters before and after swimming

The average haematocrit (Hct) percentage before swimming (eels 2003 only; $n=40$) was 31.4±1.2% (Table 1c). Total protein (TP) content was 52.8±0.9 mg/ml blood plasma. No relation existed with maturation stage (pre-

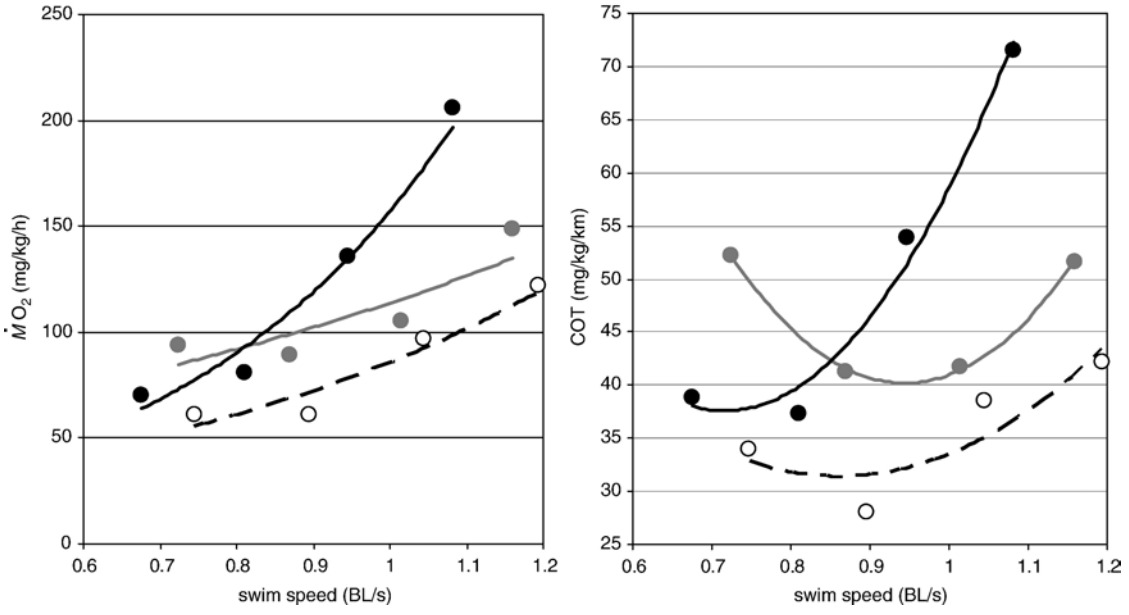


Fig. 6. $\dot{M}O_2$ and COT levels of three individual representatives: a healthy eel (dashed lines), an infected eel (grey lines) and a damaged eel (black lines).

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migrants vs. migrants). The average Hct of 32.8±0.9% after swimming was slightly higher than before but not significantly different (Table 1c). The same applied to TP content with 53.5±0.7 mg/ml blood plasma. No correlations existed between the parasite index (PI) vs. Hct and TP. Decreasing trend lines of PI vs. Hct and TP were observed, however, the values for infected eels fell well within the range of individual variation.

## 4. Discussion

### 4.1. Migratory silver eels are targets for infection

The age of the experimental eels, i.e. >12 years, was determined by otolith analysis from 20 Lake Balaton eels in a parallel study (Palstra et al., 2007). All eels were between 13 and 21 years of age. According to the classification of Durif et al. (2005), the experimental eels in this study were residents (FII) or pre-migrants (FIII), and 40% were active migrants (FV). The migrant stage FIV was not represented, indicating that silvering does not induce pectoral fin changes in this population. The high percentage of active migratory Lake Balaton silver eels contrasts with Bíró (1992), who stated that Lake Balaton eels never become silver and do not migrate. Also Székely et al. (1991), Molnár et al. (1991, 1993), Békési et al. (1997), Nimeth et al. (2000), Sures et al. (2001) and Vettier et al. (2003) stated that metamorphosis and migratory activity of Balaton eels is impeded. As eels cannot leave Lake Balaton, it is quite possible that eels undergo silvering in late summer, but regress later on when they cannot migrate.

Silver eels displayed much higher infection levels than yellow eels (Fig. 3). This can be caused by a different feeding behaviour prior to silvering. Possibly eels have prior to migration a strong appetite for fish. A higher quantity and quality of food is important to build up the energy stores required for the long journey. However, prey fishes are intermediate hosts for the larvae of *A. crassus*. As the highest infection levels of Lake Balaton eels are always found at the end of the summer — at the time of silvering, it appears that especially eels in the pre-stage of silvering are targets for infection with *A. crassus*.

### 4.2. Infection and damage

High numbers of parasites ($n>20$) were found in the larger swim-bladders, while low numbers were usually found in the shorter swim-bladders. This suggests that the density of parasites in the swim-bladder is constrained by space, which is also described by several authors (van Banning and Haenen, 1990; Ashworth and Kennedy, 1999; Lefebvre et al., 2002a,b). Recently, Lefebvre and Crivelli (2004) showed explicitly that the infection level is significantly lower in eels with severely damaged swim-bladders. We found that shortest swim-bladders did not even contain any parasites. The damage in these swim-bladders was so high that they were considered to be totally dysfunctional. It seems plausible that this stage represents the terminal phase for all heavily infected swim-bladders. The space in the swim-bladder has become very limited by the thickened walls in the shortened swim-bladder, reducing the chance for parasite survival and making re-infection very unlikely.

*A. crassus* potentially has a dual effect on its host, i.e. energy drain and swim-bladder damage. This study attempted for the first time to differentiate these effects on swimming abilities. It was assumed that a high infection level impairs the eel's endurance by the continuous energy drain — resulting in lower energy stores and a diseased state. On the other hand, the damage to the swim-bladder should impair buoyancy control. The latter is not necessarily related to the presence of parasites, as thickening of the bladder and volume reduction restricts conditions for the parasites. In this study we used the relative parasite weight as a parameter for infection level and the swim-bladder length as a parameter for the degree of swim-bladder damage.

### 4.3. Effects on blood parameters

We did not find significant correlations between infection, haematocrit (Hct) and total protein (TP) content. Results in literature are contradictory. Boon et al. (1989) did not find a significant correlation with Hct but in a later publication they found negative correlations with Hct and proteins (Boon et al., 1990b). Höglund et al. (1992) did not find a correlation with Hct but these authors did find a significant positive correlation between infection and TP. Kelly et al. (2000) did not find at all significant correlations between infection and Hct, plasma glucose and many other physiological parameters. Würtz et al. (1996) concluded that it does not seem that parasites show any sanguivorous activities but feed instead on surrounding tissue (Polzer and Taraschewski, 1993). Thus, evidence about sanguivorous activities of the swim-bladder parasite remains controversial. Still, the parasites feed on the host's energy sources and will certainly be a major negative factor when energy sources are critical such as during its spawning migration.

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### 4.4. Effects on swimming speed, efficiency and endurance

Maximum aerobic speeds ($U_{crit}$) in this study were up to 1.64 BL/s, which were comparable to those found for eels from other locations (Palstra et al., 2006a). $U_{crit}$ values were negatively correlated with infection and damage levels, though not significantly different (Fig. 5c). However, in comparison with the healthy eels, the eels with damaged swim-bladders dropped out early, and most of them could not swim faster than 0.7 m/s (Fig. 5d). These results contradict those of Münderle et al. (2004), who showed that the $U_{crit}$ of small yellow eels (40.3±2.7 cm, 81±16 g — swimming max 10 min at a speed of 0.62 m/s) was unaffected by the level of parasitism. The contrast with our results may be related to the larger size and the more advanced developmental stage of our eels, but also to the longer duration of the swimming trials in our study.

For the first time, $O_2$ consumption ($\dot{M}O_2$) was measured in parasitized female silver eels swimming at various speeds. Healthy eels from this study had oxygen consumption rates comparable to those of other eels (farmed eels and wild eels from the River Loire, France; Palstra et al., 2006a). Infected eels and eels with damaged swim-bladders however, had at all speeds higher $\dot{M}O_2$ (Fig. 4) and corresponding COT levels. Hence, we can conclude that infected eels as well as eels with damaged swim-bladders are less efficient swimmers. Healthy Lake Balaton eels had their optimum swimming speeds ($U_{opt}$) at 0.75 BL/s, which is comparable to wild silver eels from other locations. For instance, migratory silver eels from River Loire (France) had a $U_{opt}$=0.74 BL/s and those from Lake Grevelingen (The Netherlands) had an $U_{opt}$=0.77 BL/s (Palstra et al., 2006a). In comparison with healthy eels, the $U_{opt}$ of infected eels was significantly lower by 18% and that of eels with damaged swim-bladders by 21%. These eels also showed a higher (not significant) cost of transport ($COT_{min}$) at $U_{opt}$ (respectively 21% and 18%). Hence, we can conclude that infected eels and eels with a damaged swim-bladder show a considerable loss of swimming endurance.

In contrast to our expectation, we found that the effects of infection level and swim-bladder damage on $U_{opt}$ and $COT_{min}$ were rather similar. We hypothesized that a high parasite level would impair primarily endurance, due to energy drain. A reduced endurance was indeed observed; in addition also a higher cost of transport was observed. We assume that the latter was caused by an additional loss of buoyancy control. We hypothesized that extensive damage would strongly reduce the functionality of the swim-bladder, either due to an increased wall thickness or to a damaged gas gland. Loss of buoyancy control should lead to an increase in the cost of transport, as eels with such swim-bladders require additional energy to compensate for their negative buoyancy. In general, compensation can be obtained from lift and from swimming upward. Lift is provided by the pectoral fins, only during swimming (Bone et al., 1999). This mechanism is also illustrated by the fact that scombroid species, that do not have a swim-bladder, must swim continuously with pectoral fins extended. As lift increases with the square of the swimming speed, this mechanism is particularly useful for fast swimming species and not so much for eels. Therefore heavy swim-bladder damage will force eels to use also the upward swimming mode, which is very inefficient. This causes more drag, increases the cost of transport, and thus reduces the maximum aerobic and optimum swimming speeds. Apart from the expected increase of cost of transport, we also observed that eels with a damaged swim-bladder had a reduced endurance. The latter may be caused by the unnatural mode of swimming, i.e., upward. The curved body position may impose extra stress on some muscles, which limits endurance. Thus the results from this study show that migrating silver eels with infected and damaged swim-bladders have reduced swimming performance.

### 4.5. Migration failure by swim-bladder parasite

In reproduction experiments with silver eels from the Loire River (France; Palstra et al., 2006b), the infection level did not diminish during 6 months in salt water. In our recirculation system, which contained salt water, there was no chance of re-infection. This means that the parasites survived longer than anticipated or that the cysts with parasite larvae gave rise to new infections. Also Székely et al. (2005) observed that during prolonged periods, no improvement in the condition of infected eels could be observed. Indications that swim-bladder damage progresses even further under salt water conditions were also described by Kennedy and Fitch (1990), Kirk et al. (2000a,b) and Kirk et al. (2002). Therefore we assume that *A. crassus* infection does not diminish during the oceanic migration of the European eel.

Since the cost of transport at optimum swimming speeds ($COT_{min}$) is about 20% higher in heavily infected eels and eels with damaged swim-bladders than in healthy eels, it is likely that they will spend at least 20% more of their energy reserves on migration. Almost 80% of the energy required as fuel for migration is delivered by burning fats (van Ginneken

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et al., 2005b). Palstra et al. (2006c) calculated that the average silver eel needs 78 g fat/kg BW (39% of the total fat stores) as fuel. A heavily infected or damaged eel may thus spend 94 g fat/kg BW (47% of the total fat stores). These increased $COT_{min}$ values for infected eels and eels with damaged swim-bladders were found at their optimum swimming speeds ($U_{opt}$) which were however also reduced by 20%. This reduction in speed will affect the duration of migration. In the Dutch situation, silver eels start their migration in autumn (October–December) and first leptocephalus larvae are found in late March–early April (McCleave, 2003). Migration should therefore be completed within 6 months. Silver eels are likely to cruise at their optimum swimming speed, since this represents swimming at the highest efficiency (lowest COT). When we assume that eels continuously cruise at $U_{opt}$, the trip would take only 3.5 months (Palstra et al., 2006a). The 20% lower $U_{opt}$ of infected eels and eels with damaged swim-bladders may cause them to cruise slower, which extents the swimming period to about 4.2 months. This may still be in time for reproduction, although we do not know how long the animals need for final maturation and for finding the actual spawning site. Eels could also compensate for the loss of $U_{opt}$ by swimming faster, but that will result in an exponential increase of the COT (Brett, 1964). The increase in $COT_{min}$ thus burdens the energy budget and reduces migration speed.

Migration failure of infected eels and eels with damaged swim-bladders was observed in a recent study with Lake Balaton eels by Palstra et al. (2007). They subjected similar sized female silver eels ($n=21$) to simulated migration of two and six weeks swimming at a speed of 0.5 BL/s in fresh water. Six eels showed problems swimming and did not reach the 1000-km border, corresponding to 4.8 weeks. Further analysis of the swim-bladders showed that 50% were infected, and 83% were heavily damaged. This explains the poor swimming performance of these animals. In addition, it confirms the negative interference of the parasite with swimming in general. When parasitized eels manage to reach the spawning grounds in time, another problem arises. Besides the 78 g fat/kg BW for fuelling migration, another 57 g fat/kg BW is required for incorporation in oocytes (Palstra et al., 2006c). So, a total of 135 g fat/kg BW is the estimated requirement for healthy migrating silver eels. Heavily infected eels and eels with a damaged swim-bladder however, will spend more energy for migration, leaving less fat for egg production.

The swim-bladder parasite has been spread widely over Europe. In most European habitats 40 up to 90% of the eel population is infected (Sprengel and Lüchtenberg, 1991; Würtz et al., 1998; Lefebvre et al., 2002a,b; Audenaert et al., 2003; Dekker, 2004; Lefebvre and Crivelli, 2004). In this study the migratory silver eels were significantly more infected than the others, which clearly aggravates the impact of the infection on reproductive migration. Infection with *A. crassus* apparently lasts rather long even without re-infection, which makes it unlikely that silver eels will cure during migration. In this study it is shown that infection and damage of the swim-bladder impair swimming performance and increase overall energy consumption. Thus the swim-bladder parasite is a serious threat for the reproductive success of infected and previously infected European eels. We consider it therefore likely that *A. crassus* played a role in the current collapse of the European eel population.

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