Relationship between European eel *Anguilla anguilla* infection with non-native parasites and swimming behaviour on encountering accelerating flow

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The effect of *Anguillicola crassus*, *Pseudodactylogyrus bini* and *Pseudodactylogyrus anguillae* infection on the behaviour of downstream migrating adult European eels *Anguilla anguilla* as they encountered accelerating water velocity, common at engineered structures where flow is constricted (*e.g.* weirs and bypass systems), was evaluated in an experimental flume. The probability of reacting to, and rejecting, the velocity gradient was positively related to *A. crassus* larval, adult and total abundance. High abundance of *Pseudodactylogyrus* spp. reduced this effect, but *A. crassus* was the strongest parasitic factor associated with fish behaviour, and abundance was positively related to delay in downstream passage. Delayed downstream migration at hydraulic gradients associated with riverine anthropogenic structures could result in additional energetic expenditure for migrating *A. anguilla* already challenged by *A. crassus* infection.

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INTRODUCTION

Recruitment of the European eel *Anguilla anguilla* (L. 1758) has declined by >90% since the early 1980s (ICES, 2013) and the stock is considered outside safe biological limits (ICES, 1999). A number of factors have been suggested as contributors to explain this decline, including oceanic conditions (Baltazar-Soares *et al.*, 2014), overfishing (Moriarty & Dekker, 1997), pollution (Robinet & Feunteun, 2002), habitat fragmentation (Winter *et al.*, 2006), parasitism and disease (Kirk, 2003; Ginneken *et al.*, 2005). Ultimately, there is no consensus over the cause and it appears likely that

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a combination of factors led to the population crash and continue to prevent recovery (Feunteun, 2002).

Three eel specific parasites, *Pseudodactylogyrus anguillae*, *Pseudodactylogyrus bini* and *Anguillicola crassus*, were introduced to Europe through the eel trade in the late 1970s and early 1980s and spread rapidly across the continent (Kirk, 2003; Buchmann, 2012). *Anguilla anguilla* is more susceptible to these invasive parasites than the original host, the Japanese eel *Anguilla japonica* Temminck & Schlegel 1846. As a result, their intensities can become unusually high (Taraschewski, 2006; Fang *et al.*, 2008) and cause greater pathogenic effects than native parasite species (Kennedy, 2007).

Pseudodactylogyrus anguillae and *P. bini* are gill monogeneans specific to eels. At very high intensities, their attachment and feeding on host epithelia and mucus can cause haemorrhaging, hyperplasia of tissue and fusion of lamellae, reducing gill surface area and impairing respiration (Chan & Wu, 1984; Abdelmonem *et al.*, 2010). In wild *A. anguilla*, their abundance was negatively related to body condition (Gérard *et al.*, 2013). Pathogenic effects of infection are more common in high density farmed conditions (Kennedy, 2007) and severe cases can cause decreased feeding, lethargy, movement to the water surface and areas of low water velocity, and impingement on outlet screens (Buchmann, 2012). Although there is currently little evidence to expect *P. anguillae* and *P. bini* will affect *A. anguilla* migration success, there is the potential for cumulative energetic effects when *A. crassus* intensity is also high (Køie, 1991).

Juvenile *A. crassus* nematodes migrate from the eels' gut to the swimbladder wall, before entering the lumen as adults where they feed on the host's blood and tissue (Banning & Haenen, 1990). Movement and feeding can lead to inflammation, oedema, fibrosis and haemorrhaging of the swimbladder wall, resulting in a reduced (or in severe cases, collapsed) lumen and altered gas composition (Banning & Haenen, 1990; Molnár *et al.*, 1993; Würtz *et al.*, 1996). Infection can negatively affect the swimming performance of adult *A. anguilla* (see Palstra *et al.*, 2007), although conflicting results have been given (Nimeth *et al.*, 2000; Münderle *et al.*, 2004). Reduced swimming performance, in combination with organ damage and the energetic costs of sanguivorous activity, is believed likely to reduce the probability of migratory *A. anguilla* reaching their spawning grounds in the Sargasso Sea (Palstra *et al.*, 2007; Barry *et al.*, 2014). It is also suggested that the infected individuals may favour shallow coastal areas where possible to ease demand on the compromised swimbladder (Sjöberg *et al.*, 2009). The relationship between *A. crassus* infection and *A. anguilla* swimming behaviour in freshwater, however, is unknown.

During freshwater *A. anguilla* migrations, barriers, including dams, weirs and sluices, can block access to upstream habitat for colonizing juvenile and resident life stages (Moriarty & Dekker, 1997) and impair escapement of adults to sea (Calles *et al.*, 2010). Hydraulic conditions commonly encountered within these engineered river systems, such as areas of abrupt acceleration of flow (*e.g.* at weir crests, dam forebays, culvert inlets and the entrance to bypass systems), can delay downstream migration of other families, such as salmonids, by inducing behavioural avoidance and retreat upstream (Kemp *et al.*, 2006, 2008; Enders *et al.*, 2009). A number of telemetry studies have reported that *A. anguilla* entering dam forebays often move back upstream several times before selecting a downstream route of passage (Brujis & Durif, 2009). It is unclear whether this behaviour was induced by avoidance of hydraulic conditions, or occurred after contact with physical structures, such as debris screens (Jansen *et al.*,

2007). Delays of several days to weeks have been observed (Pedersen *et al.*, 2012; Piper *et al.*, 2013), which could increase the energetic cost of migration and predation risk (Rieman *et al.*, 1991; Caudill *et al.*, 2007), thus reducing the probability of individuals reaching their spawning grounds. Additionally, repellent effects at bypass entrances where flow is constricted will enhance the probability of passage through turbines and associated mortality (Castro-Santos & Haro, 2003; Calles *et al.*, 2010). Quantifying the extent and causes of behavioural avoidance is important if negative effects of river infrastructure are to be mitigated.

Both parasite infection and delay at barriers to downstream migration have the potential to deplete the energy reserves of *A. anguilla* embarking on their 5000–6000 km spawning migration, during which they do not feed. Therefore, a better understanding of *A. anguilla* response to hydraulic cues at anthropogenic structures, and exploration of the influence of parasites on freshwater migratory behaviour is required. This study investigated the potential effect of *Pseudodactylogyrus* spp. and *A. crassus* infection on the behaviour, and consequently delay, of downstream moving *A. anguilla* as they encountered an accelerating velocity gradient. It was predicted that fish energetically compromised by invasive parasites would behave passively to minimize costs associated with delay.

MATERIALS AND METHODS

FISH COLLECTION AND HUSBANDRY

Actively migrating adult *A. anguilla* ($n = 175$, total length $L_T = 589 \pm 81$ mm, mass $M = 396 \pm 188$ g, mean $\pm$ S.D.) were caught at a permanent eel trap on the River Avon (Hampshire), U.K., and transported in oxygenated tanks the following day (6 October 2010) to the International Centre for Ecohydraulics Research laboratory, University of Southampton. Only six individuals had an eye index (I_E) less than the minimum threshold (6·5) used to define the silver life stage (Pankhurst, 1982) ($I_E = 9·18 \pm 1·82$, mean $\pm$ S.D.), and all except two had an $L_T > 450$ mm, and were, therefore, presumed to be females (Durif *et al.*, 2005). All individuals were included in trials. Fish were held in a 3000 l holding tank, under natural photoperiod (50·96° N) and temperature (13·3 $\pm$ 1·4° C, mean $\pm$ S.D.).

EXPERIMENTAL SETUP AND PROTOCOL

Experiments were conducted in a re-circulatory flume (21·4 m long, 1·37 m wide, 0·6 m deep), with a maximum flow capacity of $0·47$ m^3 s^{-1}. A 1 m long velocity gradient (zone B, Fig. 1) leading to a constricted channel (4 m long, 0·77 m wide; zone C, Fig. 1) was created. Three-dimensional water velocities were recorded at 60% depth using an Acoustic Doppler Velocimeter (Nortek AS; www.nortek-as.com) sampling at 50 Hz for 60 s, with a sample depth of 3·1 mm. Spurious data were filtered using a maximum and minimum threshold filter (Cea *et al.*, 2007). The mean longitudinal velocity at each point was plotted in ArcGIS 9.3 (www.arcgis.com) and interpolated using spline methods. The configuration and velocities were representative of those at downstream fish-bypass entrances (Gosset *et al.*, 2005; Turnpenny & O'Keeffe, 2005). Assuming a linear gradient, velocity acceleration was 0·45 m s^{-2}. Water depth was maintained at 0·24 m. Flume-water temperature was 13·9 $\pm$ 1·4° C (mean $\pm$ S.D.), which is within the upper range of river temperatures during adult silver *A. anguilla* downstream migrations (Brujis & Durif, 2009).

Trials took place during darkness (1900 to 0300 hours) between 12 October and 3 November 2010. Individual *A. anguilla* were allowed a minimum of 1 h to acclimatize to flume conditions prior to release 7 m upstream of zone B and given 30 min to volitionally move downstream. The
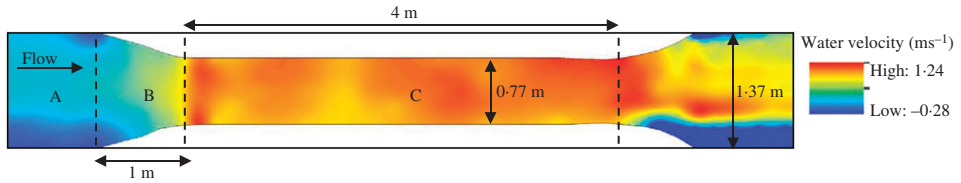
FIG. 1. Plan of flume configuration at the International Centre for Ecohydraulics Research, University of Southampton. The velocity profile created was used to assess the behavioural response of downstream moving *Anguilla anguilla* to accelerating flow caused by a constricted channel. Fish were released 7 m upstream of zone B and behaviour was quantified as they experienced the accelerating velocity in zones B and C. Mid channel velocity increased from 0·46 to 1·07 m s^{-1} over 1 m in zone B. Velocity was measured using an acoustic doppler velocimeter.

assignment of fish to consecutive trials was based on order of capture from the holding tank. Low light cameras were used to record behaviour under infrared illumination (850 nm).

POST-MORTEM EXAMINATION AND BEHAVIOURAL ANALYSIS

Following behavioural trials, *A. anguilla* were transported to Cardiff University or the Environment Agency, Brampton, and killed by an overdose of benzocaine. A parasite screen of the gills, swimbladder, spleen, gallbladder, heart, musculature and intestinal tract, using low and high-powered microscopy, allowed the overall parasite burden to be assessed for the majority of individuals (Table I). A reduced screen to evaluate abundance of invasive parasites only was conducted for 27 fish (*n* limited by time availability) and parasite data were not collected for 11 fish due to loss of their identification tags during transport. Where appropriate, parasites were fixed, cleared or stained to confirm identification (Brown *et al.*, 1986; Chubb *et al.*, 1987; Moravec, 1994; Gibson *et al.*, 2002; Jones *et al.*, 2005). Parasite infection variables followed standard definitions for prevalence (percentage of sampled population infected), abundance (count per fish) and intensity (count in infected fish only) (Bush *et al.*, 1997). The abundance of *A. crassus* was split into larval, adult and total number found in the swimbladder wall and lumen. Total *A. crassus* wet mass ($M_{A.crassus}$; mg) and *A. anguilla* mass ($M_{A.anguilla}$; g) were used to calculate the parasite index I_P ($I_P = M_{A.crassus}M_{A.anguilla}^{-1}$). *Pseudodactylogyrus bini* and *P. anguillae* were not differentiated, and their total abundance was determined by doubling the count from the right gill arches, assuming equal distribution across right and left sides (Hockley *et al.*, 2011). Species richness and diversity were calculated to describe the overall parasite community. The Simpson's diversity index was calculated as $1 - D$, where $D = [\sum n(n-1)][N(N-1)]^{-1}$, where n = total number of organisms of a species and N = total number of organisms of all species. The I_E and fin index (I_F; Durif *et al.*, 2005), as indicators of silvering, the condition factor (K; Fulton, 1904) and fish age were evaluated, due to previous evidence of a relationship with *A. crassus* or *Pseudodactylogyrus* spp. abundance (Fazio *et al.*, 2012; Gérard *et al.*, 2013), or the potential to affect *A. anguilla* behaviour. Otoliths were aged using the burn-and-crack technique (Christensen, 1968).

Video recordings were analysed to quantify *A. anguilla* behaviour. Individuals were categorized into those that approached the constriction (most downstream part of body entered zone B) and those that remained upstream in zone A. Further behavioural analysis was conducted for fish that approached the constriction (*i.e.* entered zone B). Rheotactic orientation at the point of first approach was recorded as negative (facing downstream) or positive (facing upstream). Behaviour in zones B and C was categorized as: (1) passive (no visible response to the hydraulic gradient and continued downstream movement exiting zone C), (2) reactive (change in orientation from negative to positive rheotaxis and sudden increase in tail beat frequency and burst of upstream movement) or (3) rejection (reaction followed by return to the unconstricted flume, zone A). Delay was defined as the time between first approach and the point at which the fish fully exited zone C downstream. Individuals that contacted the constriction wall and

TABLE I. Summary of the internal parasite screens, illustrating the prevalence, mean and range of intensity for each species or genus, the number of *Anguilla anguilla* screened and the mean ± S.D. of the species richness and Simpson's diversity index

	Species or genus	Prevalence (%)	Mean intensity	Intensity range	Number of fish screened
Monogenea	*Pseudodactylogyrus* sp.	97	153	1−836	152
Trematoda	*Nicolla gallica*	9	2	1−3	137
Cestoidea	*Bothriocephalus claviceps*	8	2	1−3	137
Nematoda	*Anguillicola crassus* total (swimbladder)	82	9	1−58	164
	Adult (swimbladder)	76	8	1−47	164
	Larvae (swimbladder)	50	3	1−34	164
	Larvae (gut)	4	1	1−2	137
	Spinitectus inermis	14	8	1−30	137
	Raphidascaris acus	8	1	1−2	137
	Daniconema anguillae	1	11	2−20	137
	Pseudocapillaria sp.	1	2	2−2	137
	Camallanus lacustris	1	1	1−1	137
	Eustrongylides sp.	1	1	1−1	137
Acanthocephala	*Pomphorhynchus laevis*	26	4	1−41	137
	Acanthocephalus lucii	9	2	1−3	137
	Acanthocephalus anguillae	1	1	1−1	137
Species richness mean ± S.D. = 2·62 ± 1·00					128
Simpson's diversity index mean ± S.D. = 0·20 ± 0·18					128

startled were not included in behavioural analysis (21 individuals) as it was unclear whether their response was due to the hydraulic conditions or physical contact.

DATA ANALYSIS

To avoid multicollinearity in regression models and to explore possible relationships that could influence *A. anguilla* behaviour, correlations between *A. crassus* infection variables (larval, adult and total abundance, and I_P) and *Pseudodactylogyrus* spp. abundance, and between the invasive parasite infection variables and *A. anguilla* age, L_T, M, K, I_E, and I_F, were tested for using Spearman's correlation coefficient (r_S).

Exact Mann−Whitney *U*-tests were used to test for differences in *A. crassus* and *Pseudodactylogyrus* spp. infection variables for fish that did and did not approach the constriction, and between those that approached under positive and negative rheotaxis. The effect of *A. crassus* infection parameters and *Pseudodactylogyrus* spp. abundance on the probability of *A. anguilla* *reacting* to or *rejecting* the velocity gradient during the first approach were evaluated using binary logistic regression models. Parasite species richness and diversity, water temperature, *A. anguilla* holding time (days spent in holding tanks before trial), time of trial (before 2200, 2200 to 0100 or after 0100 hours), age, L_T, M, K, I_E, I_F, rheotactic orientation on approach and two-way interactions between all invasive parasite variables were included as covariates in the initial models to account for possible effects on behaviour. Due to high correlation between some variables (L_T, M and K; I_E and I_F; I_P and *A. crassus* abundance), they were put into separate starting models and the best predictors were identified for final model development. Independent variables and interactions were selected for inclusion in the final model through a backward stepwise likelihood ratio method and examination of the Wald χ^2 statistic, to reach the minimum

adequate model with the lowest Akaike information criterion (AIC) value. Fit was assessed using likelihood ratio tests, Cox and Snell's R^2 and the Hosmer–Lemeshow test. Leverage statistics and residual analysis were used to test the validity of model assumptions. The variables found to affect *A. anguilla* behaviour were analysed for influence on the zone of reaction using Pearson's χ^2 (categorical factors) and Mann–Whitney (continuous factors) *U*-tests.

Cox regression survival analysis (Cox, 1972; Cox & Oakes, 1984; Castro-Santos & Haro, 2003) was used to assess the effect of invasive parasite abundance on delay. Main effect covariates described for logistic regression were included in the initial model and the minimum AIC value was reached through backward likelihood ratio elimination; *A. anguilla* orientation could not be included due to violation of the proportional hazards assumption (Cox, 1972). The Wald χ^2 test was used to assess for a significant effect of covariates on the hazard function, estimated by their coefficients (β). The hazard function was the instantaneous rate of downstream passage for *A. anguilla* that had not yet passed (Castro-Santos & Haro, 2003). A positive coefficient indicated a positive effect on passage rate (*i.e.* shorter delay). Individuals that did not pass within 30 min were included as censored observations.

Due to partial parasite screens for some individuals, the stepwise development of regression models to reach the minimum adequate model was conducted using only those fish with data available for all covariates. The final model was then tested with the full dataset and the results were presented. Descriptive statistics, correlation analysis and Mann–Whitney *U*-tests were conducted using all individuals with the relevant data available. All analysis was conducted using IBM SPSS Statistics 20 (www.ibm.com).

RESULTS

Prevalence of *A. crassus* was 82% ($n = 164$), intensity was $9 \cdot 4 \pm 10 \cdot 3$ (mean ± S.D.) and the maximum was 58 nematodes. Prevalence of *Pseudodactylogyrus* spp. was 97% ($n = 152$) and intensity was 153 ± 151 (mean ± S.D.), with a maximum of 836. All screened fish ($n = 152$) were infected with either *A. crassus* or *Pseudodactylogyrus* spp. Species richness ranged between 1 and 5 and all native parasites were found at much lower prevalence and intensities than *A. crassus* and *Pseudodactylogyrus* spp. (Table I). There was no correlation between *A. crassus* abundance or I_P and *Pseudodactylogyrus* spp. abundance, nor between the invasive parasite infection variables and *A. anguilla* L_T, M, K, I_E, I_F or age (r_S: $P > 0 \cdot 05$).

During the 30 min trials, 9% of fish (16 individuals) failed to approach the constriction. There was no difference in the I_P, larvae, adult or total *A. crassus* or *Pseudodactylogyrus* spp. abundance between those fish that did or did not approach the constriction (exact Mann–Whitney *U*-test: $P > 0 \cdot 05$). *Anguilla anguilla* orientation at first approach was not influenced by any of the invasive parasite infection parameters (exact Mann–Whitney *U*-test: $P > 0 \cdot 05$).

Discounting fish that contacted the constriction, 54% of *A. anguilla* that approached the constriction ($n = 138$) moved downstream passively on first approach (Table II). A reaction to accelerating velocity on first approach was displayed by 46% of *A. anguilla* approaching the constriction ($n = 138$). Rejection of the hydraulic gradient and return upstream to the unconstricted zone A occurred in 78% of all reactive fish (36% of the total approaching). Following an initial rejection of the hydraulic gradient, at least one further reaction during subsequent approaches occurred in 53% of these fish.

Anguilla anguilla that approached under positive rheotaxis were more likely to react to the hydraulic gradient than those that approached head first (Wald $\chi^2 = 22 \cdot 05$, d.f. = 1, $P < 0 \cdot 001$). All three behavioural responses to the velocity gradient were exhibited by fish infected and uninfected with *A. crassus* and *Pseudodactylogyrus* spp. The probability of *A. anguilla* reacting, however, was positively related to larval, adult and total

TABLE II. The behaviour of *Anguilla anguilla* on approach to the flume constriction. Of the 175 fish examined, 138 approached and did not startle following contact with the constriction and were included in regression models of response to accelerating flow. A further 37 that did not approach the constriction (*i.e.* remained upstream in the open channel) or contacted the structure were not included in the behavioural regression models

Behaviour	n	%
Fish included in behavioural regression models	138	
Total passive	75	54
Total reacted	63	46
Initially reacted but passed first time	14	10
Reacted and rejected constriction	49	36
Rejected but passed downstream during trial	30	22
Rejected and did not pass downstream within trial	19	14
Fish not included in behavioural regression models	37	
No approach	16	43
Excluded due to contacting the constriction	21	57
Grand total	175	

A. crassus abundance (Fig. 2), with larval abundance maintained in the final model [Wald $\chi^2 = 11\cdot19$, d.f. = 1, $P < 0\cdot01$; Table III(a)]. There was an interaction between *A. crassus* larvae and *Pseudodactylogyrus* spp. abundance (Wald $\chi^2 = 7\cdot34$, d.f. = 1, $P < 0\cdot01$); a high *Pseudodactylogyrus* spp. abundance reduced the probability of a reaction for *A. anguilla* with a high *A. crassus* abundance. The probability of rejection was increased by positive rheotaxis [Wald $\chi^2 = 33\cdot60$, d.f. = 1, $P < 0\cdot001$; Table III(b)]. The minimum AIC model for rejection also included a positive effect of *A. crassus* larvae abundance (Wald $\chi^2 = 8\cdot09$, d.f. = 1, $P < 0\cdot01$), and an interaction between *A. crassus* larval abundance and *Pseudodactylogyrus* spp. abundance (Wald $\chi^2 = 5\cdot51$, d.f. = 1, $P < 0\cdot05$). There was no effect of parasite richness or diversity, water temperature, time of trial, *A. anguilla* holding time, age, L_T, M, K, I_E or I_F on the probability of a reaction or rejection occurring.

Slightly higher numbers of *A. anguilla* reacted in zone B than in C (60 and 40%, respectively). Fish that approached under positive rheotaxis were more likely to react in zone B ($\chi^2 = 16\cdot72$, d.f. = 1, $P < 0\cdot001$). There was no effect of the invasive parasite variables on zone of reaction (Mann–Whitney *U*-test: $P > 0\cdot05$).

Of the fish that rejected the constricted channel ($n = 49$), 39% did not pass downstream within the 30 min trial. Delay was positively affected by total and larval *A. crassus* abundance; in the minimum AIC model, a negative coefficient ($\beta = -0\cdot21$, Wald $\chi^2 = 7\cdot17$, d.f. = 1, $P < 0\cdot01$) revealed that high *A. crassus* larval abundance resulted in a slower passage rate (model $\chi^2 = 9\cdot55$, d.f. = 3, $P < 0\cdot05$). Neither *Pseudodactylogyrus* spp. abundance nor the interaction between *A. crassus* and *Pseudodactylogyrus* spp. abundance affected delay (*Pseudodactylogyrus* spp.: Wald $\chi^2 = 0\cdot39$, d.f = 1, $P > 0\cdot05$; interaction: Wald $\chi^2 = 3\cdot18$, d.f. = 1, $P > 0\cdot05$). There was no effect of parasite richness or diversity, water temperature, *A. anguilla* holding time, time of trial, age, L_T, M, K, I_E, or I_F on delay ($P > 0\cdot05$).
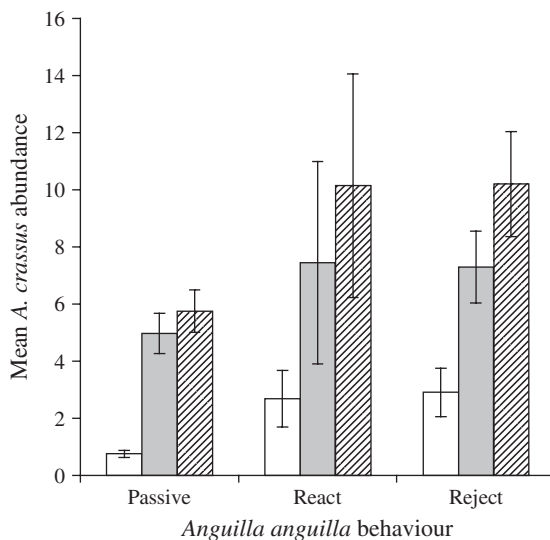
FIG. 2. The mean ± s.e. abundance of larvae (□), adult (▨) and total (▨) *Anguillicola crassus* in *Anguilla anguilla* that exhibited passive (*n* = 69), reaction (change in orientation and burst of upstream swimming followed by downstream movement, *n* = 13) or rejection (reaction followed by return upstream to the unconstricted flume, *n* = 47) behaviour on encountering accelerating water velocity during the first approach.

DISCUSSION

Contrary to the prediction made, abundance of *A. crassus* was positively related to the probability of downstream moving *A. anguilla* avoiding accelerating water velocity and retreating back upstream. While high abundance of *Pseudodactylogyrus* spp. reduced this effect, metrics describing *A. crassus* infection provided the strongest relationships with behaviour and were associated with delay to downstream passage. This demonstrated, for the first time, a possible energetic cost of *A. crassus* infection induced through host behavioural change. When combined with a decreased swimming performance (Palstra *et al.*, 2007) and impaired swimbladder function (Würtz *et al.*, 1996), this could reduce the probability of *A. anguilla* successfully completing their spawning migration.

Invasive parasites often have higher virulence and greater pathogenic effects in a novel host (Britton *et al.*, 2011; Meeus *et al.*, 2011; Lymbery *et al.*, 2014), which can lead to behavioural changes as a by-product of infection (Taraschewski, 2006; Fang *et al.*, 2008). In this study, behavioural differences associated with high intensities of invasive parasites were observed in *A. anguilla*. Although prevalence has stabilized and intensities decreased in some areas of Europe since an initial peak following introduction (Kangur *et al.*, 2010; Bernies *et al.*, 2011), intensities of *A. crassus* in *A. anguilla* remain high compared with those in wild and farmed *A. japonica* (Münderle *et al.*, 2006; Han *et al.*, 2008). *Pseudodactylogyrus bini* and *P. anguillae* are also found at greater intensities and appear to mature faster in *A. anguilla* (Fang *et al.*, 2008). *Anguilla japonica* has evolved defence mechanisms for *Pseudodactylogyrus* spp. and *A. crassus*, as indicated by frequent observation of dead encapsulated *A. crassus* larvae

TABLE III. Minimum adequate models for predicting the probability of *Anguilla anguilla* (a) reacting to the velocity gradient (change in orientation or burst of upstream swimming) or (b) rejecting (reaction followed by return upstream to the unconstricted zone A; Fig. 1)

Final model variables	β (S.E.)	Wald χ^2	P	Odds ratio ($\pm$95% C.I.)
(a) Reaction*				
Orientation during approach	4·10 (0·87)	22·05	<0·001	60·34 (10·90−334·05)
Anguillicola crassus larvae abundance	1·32 (0·40)	11·19	0·001	3·76 (1·73−8·16)
Pseudodactylogyrus spp. abundance	0·001 (0·002)	0·47	0·493	1·001 (0·998−1·005)
Anguillicola crassus larvae and *Pseudodactylogyrus* spp. interaction	−0·007 (0·003)	7·34	0·007	0·99 (0·99−1·00)
(b) Rejection†				
Orientation during approach	3·96 (0·68)	33·60	<0·001	52·42 (13·74−199·91)
Anguillicola crassus larvae abundance	0·76 (0·27)	8·09	0·004	2·14 (1·27−3·61)
Pseudodactylogyrus spp. abundance	0·003 (0·002)	1·73	0·188	1·003 (0·999−1·006)
Anguillicola crassus larvae and *Pseudodactylogyrus* spp. interaction	−0·005 (0·002)	5·51	0·019	0·995 (0·991−0·999)

*$\chi^2 = 71\cdot08$, d.f. = 4, $P < 0\cdot001$, Cox & Snell $R^2 = 0\cdot45$, Hosmer & Lemeshow $\chi^2 = 8\cdot68$, d.f. = 8, $P > 0\cdot05$.
†$\chi^2 = 65\cdot66$, d.f. = 4, $P < 0\cdot001$, Cox & Snell $R^2 = 0\cdot43$, Hosmer & Lemeshow $\chi^2 = 10\cdot23$, d.f. = 8, $P > 0\cdot05$.

in both naturally and experimentally infected fish (Knopf & Mahnke, 2004; Münderle *et al.*, 2006).

Avoidance of accelerating flow is probably an evolutionary response to natural constrictions or waterfalls, exhibited by fishes where there is the potential for injury or disorientation and increased susceptibility to predation (Kroese & Schellart, 1992; Enders *et al.*, 2009). Adult *A. anguilla* with an *A. crassus* intensity >10 were observed to have a 19% reduction in maximum swimming speed (Sprengel & Lüchtenberg, 1991). As velocities in the constricted section of flume approached the maximum threshold of average adult *A. anguilla* burst swimming performance (Clough *et al.*, 2004), the greater avoidance of this area by fish hosting a high abundance of *A. crassus* may have reflected efforts to compensate for a lower ability to escape danger. Alternatively, variation in parasite burden may have been a result of intrinsic differences in behaviour between individuals, which influenced the probability of infection. For example, a positive relationship between *A. crassus* abundance or swimbladder damage and *A. anguilla* body condition or size relative to age (Lefebvre *et al.*, 2012; Gérard *et al.*, 2013) may be linked to levels of foraging activity rather than a consequence of infection. More active fish may consume more paratenic hosts and increase the probability of *A. crassus* infection (Lefebvre *et al.*, 2013).

Various energy conservation strategies have been observed in parasitized fishes with reduced swimming ability (*e.g.* later flight response to a threat, Binning *et al.*, 2014;

limited dispersal range, Horký *et al.*, 2014). Gill damage from *Pseudodactylogyrus* spp. in aquaculture conditions can cause reduced activity levels (Buchmann, 2012). The current study supports a more passive, energy saving behaviour in wild *A. anguilla* heavily infected with *Pseudodactylogyrus* spp., shown by the interaction effect between *Pseudodactylogyrus* spp. and *A. crassus* abundance. As the influence of *Pseudodactylogyrus* spp. on *A. anguilla* behaviour was only apparent when *A. crassus* abundance was high, this suggests that when combined with an additional stressor, infection by *Pseudodactylogyrus* spp. could affect *A. anguilla* behaviour. Further study is required to fully understand the behavioural strategies employed by fish heavily infected with *A. crassus* in isolation *v.* those with high intensities of *Pseudodactylogyrus* spp., relative to control uninfected fish. Furthermore, the influence of previous infection and organ damage on behaviour should be considered.

Although a much lower proportion of *A. anguilla* (46%) showed a reaction or rejection to the velocity gradient than similar laboratory studies have reported for salmonids (*e.g.* up to 95% of brown trout *Salmo trutta* L. 1758; Vowles & Kemp, 2012), this indicates that *A. anguilla* will respond to hydraulic cues as well as physical structures. Furthermore, a greater avoidance of velocity gradients at dam bypass entrances will reduce passage efficiency for *A. anguilla* parasitized with *A. crassus* and increase delay. This should be accounted for in future bypass design to ensure that the hydraulic conditions at the entrance encourage efficient downstream *A. anguilla* passage. To achieve this, further research on *A. anguilla* behaviour at different velocity gradients is required both in controlled laboratory conditions and *in situ*.

To complete their spawning migration *A. anguilla* travel up to 6000 km, during which they do not feed (Schmidt, 1923; Tesch, 2003), and must maintain sufficient energy reserves for successful reproduction (Thillart *et al.*, 2008). Infection with *A. crassus* elevates the cost of swimming at optimal speeds by *c.* 20%, demonstrating an energetic cost which presumably will affect *A. anguilla* throughout their migration (Palstra *et al.*, 2007). Although the effect of *P. bini* and *P. anguillae* on swimming performance has not been investigated, it is feasible that an impairment to respiration could exacerbate the effects of *A. crassus* to increase demand on energy stores. This study demonstrates a further possible energetic cost due to *A. crassus* infection. Delay as a result of rejecting the constricted flume was relatively short due to limitations of the experimental duration and 86% of *A. anguilla* that approached the constriction without contacting the structure passed downstream within the trial. There was, however, a limited area within which fish could seek alternative routes. *In situ* radio-telemetry studies have shown that downstream migrating eel can be delayed from a few minutes to several weeks at dams where hydraulic gradients are common (Haro *et al.*, 2000; Winter *et al.*, 2006; Jansen *et al.*, 2007). *Anguilla anguilla* occasionally retreat upstream several kilometres before returning to the dam (Pedersen *et al.*, 2012) and can approach several times before finally passing downstream (Behrmann-Godel & Eckmann, 2003; Travade *et al.*, 2010). Furthermore, as European rivers are heavily fragmented by anthropogenic structures, the cumulative effect of multiple delays could be considerable (Piper *et al.*, 2013), although no data are currently available to quantify the effect on energetic costs, lipid reserves or spawning success. The results of the current study suggest that the combined effect of barriers and parasite infection on energetic costs during migration should be recognized in *A. anguilla* conservation efforts to promote passage, escapement and spawner quality.

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