Comparison of attraction, entrance and passage of downstream migrant American eels (*Anguilla rostrata*) through airlift and siphon deep entrance bypass systems

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Abstract

Downstream migrating anguillid eels face many barriers including turbines and pumps at impoundments for water abstraction, power generation and water level control, when attempting to exit the freshwater catchment to reach spawning grounds. Multiple eel species worldwide are facing different levels of endangerment and alleviating the impacts of barriers to migration is essential to allow completion of the life cycle. Deep bypass systems with entrances located near the riverbed hold some promise for increased effectiveness compared to traditional downstream guidance and bypass facilities with entrances near the surface, as eels typically occupy the bottom of the water column. Here we evaluate two deep entrance bypass designs; an airlift (the Conte Airlift) and a conventional gravity siphon of the same entrance dimensions. Tests were performed using migratory silver-phase American eels (*Anguilla rostrata*), at night, in a simulated forebay environment. Passage performance was monitored over a 3 h test period using both PIT (passive integrated transponder) tag and video recording equipment. Entrance velocity was fixed at 1.2 m/s in each of 8 test runs with cohort size fixed in six runs at 14 and in two runs at 42. Test eels readily located, entered and passed both bypass designs. Differences in performance metrics between the airlift and siphon were not statistically significant ($P>0.05$) with linked mean values of 74.5%, 90.5% and 100%, respectively. Eel length did not affect passage speed ($P>0.05$) or slip ratio, i.e., the measured eel velocity relative to fluid velocity. The slip ratio was, however, greater in the siphon than in the airlift ($P<0.01$) within identical vertical upflow sections of the test equipment. Siphon slip ratios in the upflow vertical section were comparable to those established for the horizontal and downflow sections. Fish density did not affect attraction and passage through the airlift or siphon. No mortality or signs of injury were observed on any of the test eels through a 48 h post-test observation period. Both airlift and siphon downstream bypass systems show promise as effective technologies for protection of downstream migrating eels at a variety of water diversion or hydroelectric sites that pose threats of impingement, entrainment, and turbine mortality.

1 Introduction

Freshwater eels are of global concern following a 40-year drastic decline in recruitment of several eel species (Dekker and Casselman, 2014; Miller et al., 2015). They have a complex catadromous life cycle and must navigate to oceanic spawning grounds after spending considerable time in freshwater (ranging from 6 – 60 years in for European eels (*A. anguilla*) (Tesch, 2003) and up to 40 years for American eels (*A. rostrata*) (Miller, 2005)). During the downstream spawning migration, they face riverine barriers of many anthropogenic origins, including hydropower and pumping station intakes. The direct mortality caused by passage through turbines and pumps (Coutant and Whitney, 2000), or indirect impacts caused by delays to migration and increased susceptibility to disease and predation (Garcia De Leaniz, 2008), have undoubtedly contributed to their decline (Feunteun, 2002). Guidelines to protect eel advise that such intakes are screened, but this remediation measure is expensive (Electric Power Research Institute (EPRI), 2001) and there is still the requirement for a safe alternative downstream passage route for eels to exit the catchment. For these reasons, there is plentiful interest from environmental managers and engineers to find a cost–effective solution to downstream eel passage.

Flow is one of the key drivers during the eel downstream spawning migration (Stein et al., 2016); this cue can be exploited by providing an attractive entrance flow and utilising the natural searching behaviour of eels. For such a bypass channel to be effective, the flow must not only attract eels but prevent them from leaving the pass in an upstream direction, whilst passing all eels with no mortality or injury. In this study, two methods of producing flow within a bypass were investigated and compared: lifting water using air and using a gravity siphon.

A typical airlift pump has a gas (usually air) injected at the base of a submerged riser tube. Gas bubbles suspended in the fluid cause the density of the fluid in the tube to be less than that of the surrounding fluid; the resulting buoyant force induces flow in the tube (Reinemann et al*.,* 1990). Airlifts are used in wastewater treatment plants for low lift, high volume applications and have previously been used for transporting live fish in aquaculture (Summerfelt et al., 2009) and for sampling migrating juvenile salmonids (Brege et al*.,* 1990). Haro et al. (2016) found that silver American eels readily located, entered, and passed through an airlift deep bypass (the Conte airlift bypass) system multiple times, with all eels passing through the bypass when the entrance velocity exceeded 1 m s^{-1}. A siphon requires a pipe or tube shaped as an inverted “U” placed between two fluids that have their surfaces at different heights, which continuously transfers fluid over the bend from the higher to the lower level through the combined effect of pressure and gravity (Richert and Binder, 2011). Siphons have been used as eel bypasses around the world. For example, Legault et al. (2003) reported 12% of the downstream migrating silver European eels passed through a siphon bypass in a reservoir in France. Boubée and Williams (2006) found a siphon used in conjunction with another free-flowing bypass passed 79% of longfin (*A. dieffenbachii*) and shortfin (*A. australis*) eels at a power station in New Zealand. However, Calles et al. (2012) found no tagged European eels passed through the siphon at a hydroelectric plant in Sweden due to failure of intake racks in preventing rapid entrainment of eels into turbines. These variable results highlight that eel bypasses require further research for effective designs to be developed.

This study aimed to compare the performance of both airlift and siphon technologies under similar controlled laboratory conditions, with attraction hydraulics (flow and flow acceleration at the bypass entrance) held constant, and to test the repeatability of the Conte airlift bypass system experiment. Slip ratio, a metric to describe the measured velocity of the eel within the airlift or siphon pipe compared to the fluid velocity in the pipe, was also estimated. Analysis of slip ratio can be used to infer if eels are swimming with or against the flow within the pipe, or drift passively.

Objectives of this study were to: 1) compare attraction, entry and passage rates of airlift and siphon bypasses; 2) quantify transit times, speed and slip ratio of eels passing through both bypasses; and 3) evaluate effects of both bypass designs on injury and mortality of passed eels. We also compared speed of passage and slip ratio through the airlift from data conducted in a similar previous (2014) study of the airlift at several entrance velocities (Haro et al 2016).

2 Methods

2.1 Airlift and Siphon Design and Operation

A small diameter bypass system that could be configured as either an airlift or gravity siphon was designed to accommodate passage of large (approximately 100 cm total length) adult silver-phase eels and constructed in the U. S. Geological Survey S. O. Conte Anadromous Fish Research Laboratory (CAFRL) Flume Facility (Turners Falls, Massachusetts, USA). Additional details of the operation of the airlift (the Conte airlift) are given in Haro et al. (2016).

The bypass systems were constructed from steel and PVC pipe and fittings and had a common 30.5 cm diameter circular entrance (Figure 1), with the floor of the airlift entrance located 11.4 cm above the floor of the flume. The entrance tapered to a 20.3 cm diameter horizontal section that transitioned to the 25.4 cm diameter vertical section (the riser pipe) via two 45° angle fittings. The vertical section of the airlift configuration extended 33.5 cm above the water surface with a total water depth of 3.84 m. For the airlift configuration, air was injected into the bottom of the vertical riser section to create a total vertical lift (from the invert of the bypass entrance to the top of the riser pipe) of approximately 4.06 m. Air was supplied to the bottom of the riser pipe from a portable rotary screw compressor powered by an internal combustion engine (Figure 1a). A valve was used to regulate the airflow from the compressor through the 2.5 cm diameter flexible airlines that terminated in a manifold consisting of four 2.5 cm diameter air injection pipes. The pipes were used to introduce air horizontally into a PVC expansion fitting between the 20.3 cm and 25.4 cm diameter pipe sections (Figure 1b).

The airlift pipe structure was modified to construct a closed-conduit, gravity siphon by connecting additional 25.4 cm diameter pipe to the top of the riser tube (Figure 2). The siphon extension consisted of adding a 90-degree elbow to the top of the riser pipe, which added 0.36 m of vertical height, transitioning to a 21.8 m long horizontal section running above the water level of the containment area, passing over a bulkhead and descending through a 4.4 m vertical section. A 90-

degree elbow then transitioned horizontally from the vertical section to a gate valve (used for establishing the siphon); flow from the siphon then exited to a 1.22 m deep tailwater section.

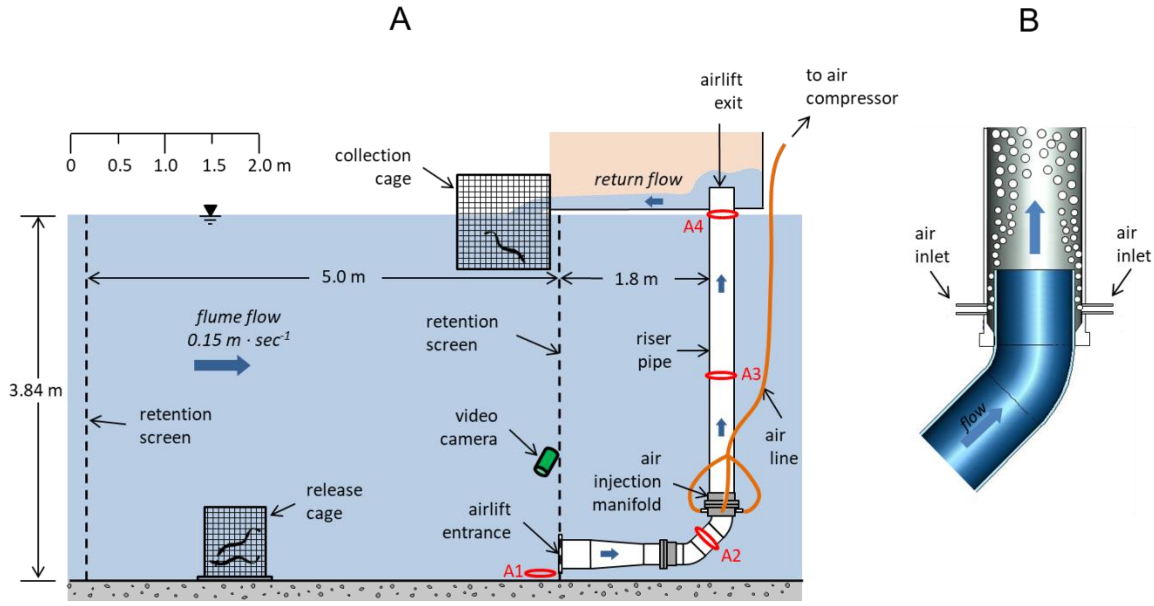

Figure 1. A). Elevation view of airlift test apparatus in the flume facility, approximately to scale. Blue arrows indicate direction of water flow. A1–A4: PIT antennas 1–4. B): cross-section of air injection manifold at base of riser pipe.

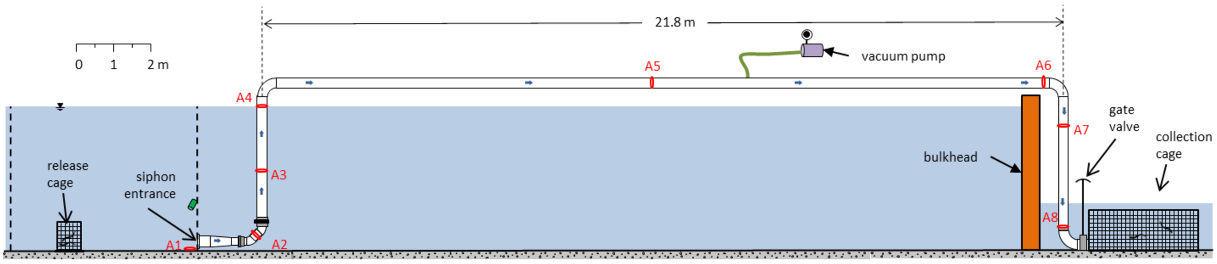

Figure 2. Elevation view of siphon test apparatus in the flume facility, approximately to scale. Note modification of airlift riser pipe to extend pipe downstream and over a bulkhead, to a submerged collection cage, and addition of four PIT antennas (A5-A8) further down the pipe. Blue arrows indicate direction of water flow. The vacuum pump enabled evacuation of air from the pipe (with downstream gate valve closed) to initiate the siphon.

2.2 Bypass hydraulics

In the previous (2014) study of the Conte airlift (Haro et al., 2016), an entrance velocity of 1.2 m s^{-1} was associated with higher entry rates than lower tested velocities. Therefore, a nominal cross-sectional water velocity of 1.2 m s^{-1} at the plane of the entrance was established for both the airlift and siphon bypasses in this study. Entrance velocity for the siphon bypass configuration was determined by measuring total flowrate through the siphon via a Signet Model 515 pipe-mounted flowmeter mounted at the centre of the horizontal section of the siphon and calculating entrance velocity based on cross-sectional area of the entrance and flowrate. To establish a gravity siphon, the containment area was filled to the working depth (3.84 m), and the downstream gate valve was closed. Air within the siphon pipe was then evacuated using a vacuum pump, then the gate valve was opened to start the siphon flow.

2.3 Biological Test Conditions

An eel containment area was created in the 6.1 m wide flume facility by constructing two 3.9 m high retention screens (1 cm plastic mesh) oriented perpendicular to the flume flow, 5.0 m apart (Fig. 1). The bypass system was installed 0.5 m away from one wall, with the entrance penetrating but flush with the downstream screen. A box made of wood at the exit of the airlift system was used to direct all flow and eels back into a collection cage (1.0 m wide by 1.0 m high by 1.0 m deep) within the containment area. For the siphon system (Fig. 2), eels passing through the siphon were directed into a submerged collection cage (3.0 m wide by 1.0 m high by 1.5 m deep) located within the tailwater section at the downstream end of the siphon pipe.

Passage of eels through the airlift and siphon was monitored with passive integrated transponder (PIT) coil antennas located at the entrance to the bypass and at several locations along the airlift (A1-A4; Fig. 1A). Four additional coil antennas (A5-A8; Fig. 1B) were positioned on the horizontal and downstream vertical sections of the siphon. PIT receivers (Texas Instruments TIRIFD model S-2000) were interfaced to a computer that logged detections of individually tagged eels within 0.25 m of each antenna to the nearest 0.1 sec. The entrance was also continuously monitored with a downward-looking underwater video camera, with the viewing area illuminated by an infrared LED illuminator (Larson Electronics LEDLB-4R-IR-MSL, 850 nm cutoff wavelength; creating infrared illumination not visible to eels; Andjus et al., 1998) and a 1 m by 1 m retroreflective background (3M Diamond Grade 3990) placed on the flume floor. Ambient nighttime light levels inside the flume from outside sky illumination through skylights were approximately 0.0015 μW cm^{-1} or less, far below locomotor synchronization thresholds for small yellow European eels (*A. anguilla*) of 20 μW cm^{-1} (van Veen and Andersson, 1982). Although these low ambient light levels may still have permitted eels to see structures within the test apparatus, the infrared illumination was considered to have no effect on attraction/repulsion to the bypass entrance, and behaviours were assumed to be representative of typical nocturnal behaviours of eels.

A cylindrical release cage (0.56 m diameter by 0.56 m high; constructed of aluminium perforated screen) which had no bottom screen was positioned in the centre of the containment area. The cage was magnetically attached to the bottom and could be lifted from the floor using an overhead hoist, allowing released eels to laterally disperse into the containment area without impediment.

Transit times of a passive particles moving through pairs of adjacent PIT antennas were calculated by dividing the calculated nominal water velocity through the pipe section between antennas (based on entrance velocity and pipe cross-sectional area and accounting for changes in pipe diameter) by the flow-path distance between PIT antennas.

2.4 Eel Collection, Holding, and Tagging

Adult, migratory American eels were collected at the downstream bypass sampler at Hadley Station, Holyoke, Massachusetts (Connecticut River; n = 54). Because of low sampler catches at Holyoke in 2015, supplemental eels were collected from commercial eel weirs in Newfoundland, Canada (Little Barachois Brook and Flat Bay Brook; n = 30) for a separate, unrelated telemetry study at a nearby hydro project. Holyoke eels were collected on 1 and 29 October 2015 between 19:00 and 23:00 h and were immediately transported to the flume facility in an aerated 500 l tank mounted in the back of a truck. Newfoundland eels were collected September 6 – 15 2015 and shipped by air freight on 21 October, held in tanks at the hydro project (supplied with flow-through ambient Connecticut River water) for 1 week (used as controls for the telemetry study), and then transported by the truck tank to the flume facility on 26 October. Handling, measurement, and tagging of eels followed protocols developed by Brown et al., (2009); fish handling was conducted in accordance with the USGS Leetown Science Center's Institutional Animal Care and Use guidelines. Eels were lightly anesthetized with a eugenol solution (Aqui-S 20E; Aqui-S New Zealand Ltd.), intraperitoneally tagged within 24 h of transport to the flume facility with 32 mm half-duplex glass-encapsulated PIT tags (Texas Instruments TIRFID system; 3 mm diameter by 32 mm in length, weight 0.8 g, 134.2 kHz), and allowed to recover from tagging for at least 48 h before testing. During tagging, total length (nearest mm) and eye diameter (horizontal and vertical; nearest 0.1 mm) were measured. Eye and total length data were collected to calculate eye indices, a measure of developmental maturity for the downstream migratory silver phase (Pankhurst, 1982). Eels were held in 2 m diameter circular tanks supplied with open flow from the Connecticut River, and provided with hiding tubes and nylon netting for cover.

2.5 Test Protocol

Eels migrate downstream primarily at night (Haro, 2003), therefore testing was initiated at dusk, with a 3 h trial from approximately 19:00 to 22:00; ambient light level within the flume facility was < 0.1 lux and were presumed to be similar for all trials. Only one trial was run per night; the siphon was tested on 3, 4, and 9 November while the airlift was tested on 5, 6, and 10 November. Three trials were performed for each bypass design with 14 eels per trial selected from both collection sites (9 Holyoke eels, 5 Newfoundland eels). To test for effect of sample size on bypass efficiency, all eels that had previously been introduced for passage through the airlift (three groups of 14) were tested in the siphon in one pooled group (i.e., one run of n = 42) and vice – versa for eels first introduced for passage through the siphon. Limited availability of wild silver eels necessitated retesting of these fish. Eels were tested in alternate bypasses to minimise potential influence of familiarity with the bypass as far as possible. The n=42 airlift trial was conducted on 12 November and the n=42 siphon trial was run on 13 November. Eels were tested this way in alternate bypass systems to minimise potential influence of familiarity of eels with the alternate bypass design. Test eels ranged in size from 526 – 1005 mm TL (mean 755 mm). Eye indices ranged from 4.9 – 11.3 mm (mean 7.7) so all eels were deemed to be silver phase (Pankhurst, 1982). Eels from Newfoundland and Holyoke collection sites were of comparable size (t-tests; t = -1.2842, df = 46.107, P = 0.2055).

Eels were transported from the holding tank to the flume inside a dark, insulated 100 l cooler, and transferred to the release cage with the flume water depth approximately 0.5 m. Flows in the flume were then increased such that total depth was 3.84 m and velocity through the screened containment area was about 15 cm · sec^{-1}. Air was then supplied to the airlift to establish the test airlift entrance velocity. Eels were allowed to acclimate to the release cage in the flume environment for 30 min and then released into the containment area by raising the release cage off the floor of the flume. Eels were allowed to volitionally explore the containment area for a total of 3 h. At the end of the test period, the flume was drained, and eels were collected using dipnets for examination of any injuries or abnormal behaviours before being transported back to the holding tank. Post-test eels were inspected every 12 h over a 48 h period for latent mortality or evidence of developing injuries. Behaviour of individually identified eels was quantified by integrating PIT detection data at all antennas (4 in the airlift bypass and 8 in the siphon bypass) with behaviours recorded at the bypass entrance via the described underwater video camera.

Eels were not included in time, speed and slip velocity calculations when video footage analysis revealed missed antennae detections at the entrance (airlift = 2 and siphon = 2). During siphon trials, twelve eels were not detected on A7 due to equipment failure and thus speed and slip ratio for A6>A7 and A7>A8 could not be calculated. There were 17 cases of crosstalk (detections of the same tag code at two antennas that were less than the antenna read rate [every 75 milliseconds]) between A6 and A7 and were removed from the dataset.

2.6 Fish pass efficiency metrics

A number of metrics were used to assess the behaviour of eels, the performance of each bypass and any difference between the bypasses (Table 1).

Table 1. Fish passage efficiency metrics

Metric	**Description**
1) Attraction efficiency	Percentage of fish that are attracted to the bypass entrance (detected on A1)
2) Entrance efficiency	Percentage of fish attracted to the bypass entrance (detected by A1) that subsequently entered the bypass pipe (detected on A2)
3) Passage efficiency	Percentage of fish that entered the bypass pipe (detected on A2) and successfully negotiated and exited the entire bypass (detected on A4 / A8)
4) Overall efficiency	Percentage of fish that were attracted to, entered and successfully negotiated the entire bypass (encompasses attraction, entrance and passage efficiency)
5) Number of approaches before passage / non-passage	Count of the number of times each fish was attracted to the bypass entrance (detected by A1), for detections greater than 15 seconds apart
6) Attraction time	Time from release to first detection at the bypass entrance (first detection on A1)
7) Entrance time	Time from release to entry (first detection on A1 during last approach event)
8) Delay between first approach and entry	Time from first approach (first detection on A1) and entry (first detection on A1 during last approach event)
9) Passage speed	Speed that eels travelled between each pair of antennae (distance between each antenna pair divided by difference in times of first detection on each antenna pair), and from bypass entrance (first detection on A1 during last approach event) to exit (first detection on A4 / A8)

2.7 Effect of slip ratio

The airlift was designed to establish fluid (air +water) velocities within the riser sufficient to entrain, lift and transport eels of varying length, weight and cross-sectional area to target release points. Fluidization or lifting will occur when drag forces exerted on inanimate objects, by rising fluid velocities, reach an equilibrium with gravity forces including net buoyancy, e.g., minimum fluidization velocities of discrete particles are related to density of the solid, density and viscosity of the fluid, packing porosity, effective particle size and uniformity coefficient (Weber, 1972). In the case of eels, additional factors must be considered including potential for thrust development as well as induced drag related to bridging. Bridging is defined here as a deliberate or random change in the orientation of the eel relative to flow direction such that drag forces at the eel body-pipe wall interface increase over that expected with an eel oriented with the current and avoiding pipe wall contact. We calculated a dimensionless slip ratio (SR) to quantify the through-pipe velocity of eels (V_{eel}) relative to fluid movement (V_{fluids}): SR = $(V_{eel})/(V_{fluids})$ within various sections of the airlift and siphon. V_{eel} was derived from transit times of eels between PIT antenna A4 and A3 as well as the pairs A5, A6 and A7, A8 monitored during siphon tests. V_{fluids} was calculated based on pipe cross sectional area, water and air flow rate assuming (1), the two-phase flow is homogeneous and (2), that gas absorption/desorption is negligible. Air flow rate was corrected for temperature and pressure using the Ideal Gas Law (to correct airflow measurements based on standard conditions (temperature = 21.1 C, pressure = 1 atm) to the conditions of pressure and temperature present at the airlift positions A3 and A4, Figure 1A.). Following the latter, air volume at the base of the riser (Antenna A3) is less than that present at the upper antenna A4. Therefore we used the log mean of V_{fluids} in our calculation of SR: $V_{fluids} = ((V_{fluids})_{A4} - (V_{fluids})_{A3}) / \ln((V_{fluids})_{A4} / (V_{fluids})_{A3})$. Slip ratio was also calculated for eels passing through the airlift bypass in the previous 2014 study at three different flows (Haro et al., 2016) for comparison between flows and between years (2014 compared to the present study) for eels passing at 1.2m s^{-1}.

2.8 Statistical analyses

Data from this study and from the 2014 airlift study (speed of passage and slip ratio data only) were analysed separately but using similar techniques. All metrics used to assess performance of bypasses were comparable between runs within treatments ($P > 0.05$), so data within each study were pooled among replicate runs for analysis. Data were tested for normality of variance using a Shapiro-Wilk Normality Test before using Welch Two Sample t-tests for normally distributed data (referred to as t-test) or Wilcoxon Signed-Rank tests for non-normally distributed data (referred to as Wilcox-test), to test for differences between two groups in metrics 5 – 9 and slip ratio (Table 1). When comparing eel orientation, passage speed between antennas and slip ratio, either one-way ANOVAs (normally distributed data) or Kruskal Wallis tests (KW-test) with a Pairwise Wilcoxon Rank Sum post- hoc test (post-hoc) (non-normally distributed data) were performed. Pearson product moment correlation was used to test for correlations between eel length, passage speed and slip ratio. Eel length and eye index were compared between collection sites and study years using t-tests.

Cox's proportional hazard regression (Allison, 1995) was used to test for differences in approach and passage rates (percentage of first approach and first pass events over time) under each of the treatments (airlift or siphon); dependent variables were time to approach and time to pass. Eels that failed to approach or pass during the trial were included as censored observations, with time set to trial duration (3 h). Proportional hazard regression was also used to compare approach and passage rates between the pooled n=14 trials and the n=42 trials.

All statistical analyses were carried out in R studio v 3.3.0 and SigmaPlot v 12.0.

3 Results

3.1 Fish pass efficiency summary metrics

The airlift had an attraction efficiency of 76.2% and the siphon 72.6% of the total number of eels released into the forebay. Of the eels attracted to the entrance, 85.9% successfully entered the airlift and 95.1% successfully entered the siphon, and all these eels successfully passed through the whole bypass (100% pass efficiency). Eels usually passed after first investigating the entrance to either bypass, with mean number of attempts before passage (airlift = 1.18 and siphon = 1.21) or non-passage (airlift = 1.33 and siphon = 1.33) being comparable (Wilcoxon test; *P* >0.05) (Table *2*).

Table 2. Summary of fish pass efficiency metrics between each bypass (three runs of n = 14 and one of n = 42, total 84 eels introduced for passage through each bypass).

Metric	Airlift	Siphon
Released (n)	84	84
Attraction efficiency (% (*n*))	76.2 (64)	72.6 (61)
Mean number of attempts before passage	1.18	1.21
Mean number of attempts before non-passage	1.33	1.33
Entrance efficiency (% (*n*))	85.9 (55)	95.1 (58)
Pass efficiency (% (*n*))	100 (55)	100 (58)
Overall efficiency (%)	**65.5**	**69.0**

3.2 Time from release to first approach, entry and passage

Eels behaved comparably after first release, upon first reaching and passing both bypasses; there was no significant difference in median bypass attraction time, median passage time or median delay time between first detection and first passage (Table 3; Figure).

Table 3. Attraction time, entrance time and delay time between first detection and passage (median ± SD, (range) and statistical analysis (Wilcox tests; W and *P* values). Time units are hour:minute:second.

	Attraction time	Entrance time	Delay between first detection and passage
Airlift	00:20:31 ± 00:42:48, (00:01:54 – 02:53:40)	00:21:12 ± 00:41:22, (00:01:54 – 02:53:40)	0 ± 00:10:26, (0 – 0:44:53)
Siphon	00:17:33 ± 00:40:00, (00:00:57 – 02:31:38)	00:27:01 ± 00:42:52, (00:00:57 – 02:51:17)	0 ± 00:24:05, (0 – 02:13:38)
Statistics	W = 2011, *P* = 0.3466	W = 1458, *P* = 0.8771	W = 1375, *P* = 0.2852

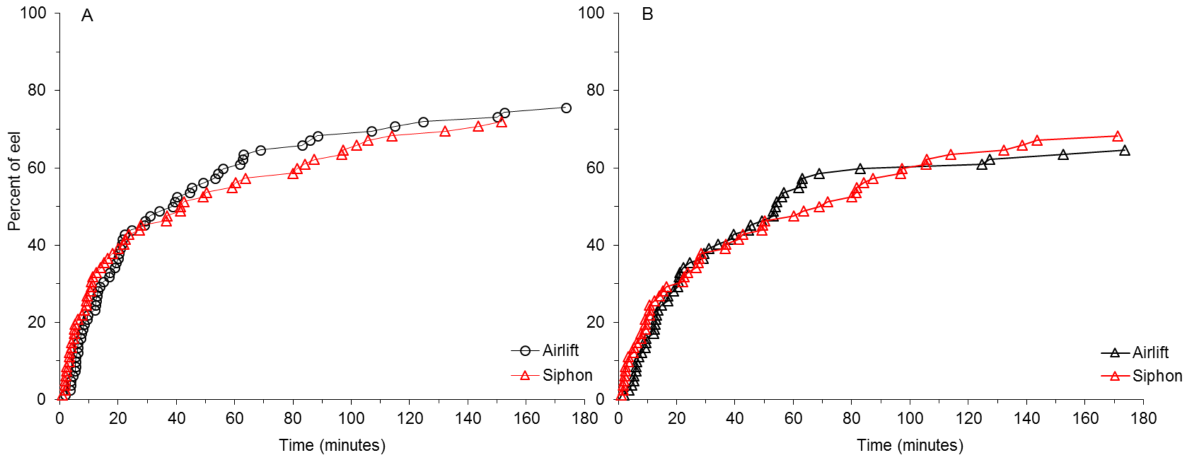

Figure 3. Cumulative time eels took to a) first approach and b) first enter (expressed as percent of eel in each trial) for each airlift and siphon test.

There was also no significant difference in rates of approach between the siphon and airlift for either the pooled n=14 (Cox's proportional hazard regression; p=0.581) or n=42 (p=0.506) trials. Similarly, there was no significant difference in rates of passage between the siphon and airlift for either the pooled n=14 (Cox's proportional hazard regression; p=0.341) or n=42 (p=0.722) trials.

3.3 Orientation of passed eels

A comparable proportion of eels that approached the airlift (62%) and siphon (57%) in head first orientation rejected entry. A higher proportion of eels that passed through the airlift (63%) and siphon (74%) entered in a head first orientation. There were fewer eels that were entrained in a tail first (airlift = 20.4% and siphon = 17.5%) or sideways (airlift = 13% and siphon = 3.5%) orientation (Table 4). Orientation of eels (head first, tail first or sideways) did not affect total passage time through the airlift (KW-test; X^2 = 39.84, df = 38, P >0.05) or the siphon (KW-test; X^2; = 55, df = 55, P >0.05).

Table 4. Count and mean number of events per eel of orientation of eels rejecting and entering the airlift and siphon bypasses

	Reject tail first		Reject head first		Enter tail first		Enter head first		Enter sideways	
	Count	Mean	Count	Mean	Count	Mean	Count	Mean	Count	Mean
Airlift	11	1.10	18	1.29	13	0.2	35	0.6	7	0.1
Siphon	10	1.25	13	1.18	11	0.2	44	0.8	3	0.1
Total	**21**		**31**		**24**		**79**		**10**	

3.4 Passage speed

Speed of eel movement through the siphon was significantly faster than the airlift in sections A1>A2 (W = 947, *P* = 0.001), A2>A3 (W = 870, *P* <0.001) but not A3>A4 (W = 1256, *P* = 0.166) (Figure 4). The overall speed through sections A1>A4 in the siphon (mean ± S.D. = 1.04 ± 0.33 m s^{-1} (min – max = 0.41 – 1.86 m s^{-1})) was significantly faster than the airlift (0.82 ± 0.34 (0.18 – 1.79 m s^{-1}; W = 2117.5, P = 0.001)). As the siphon bypass had an extra 27 m of pipe in addition to the airlift pipe section (Figure 1), speed of eels moving through these additional siphon sections was also investigated. Eels moved significantly faster through sections A5>A6 and A6>A7 of the siphon than all other sections (Kruskal-Wallis X^2 = 251.8, df = 147, *P* < 0.001; pairwise Wilcoxon post- hoc tests, *P* <0.001) but were comparable to each other (*P* >0.05). Speed through the siphon was the most variable between antennae sections A2>A3 (0.2 – 2.7 m s^{-1}) and A6>A7 (1.4 – 4.8 m s^{-1}). There was no significant correlation between eel length and passage speed through any section in any of the trials in 2014 or 2015 (*P* >0.05; Pearson product moment correlation).

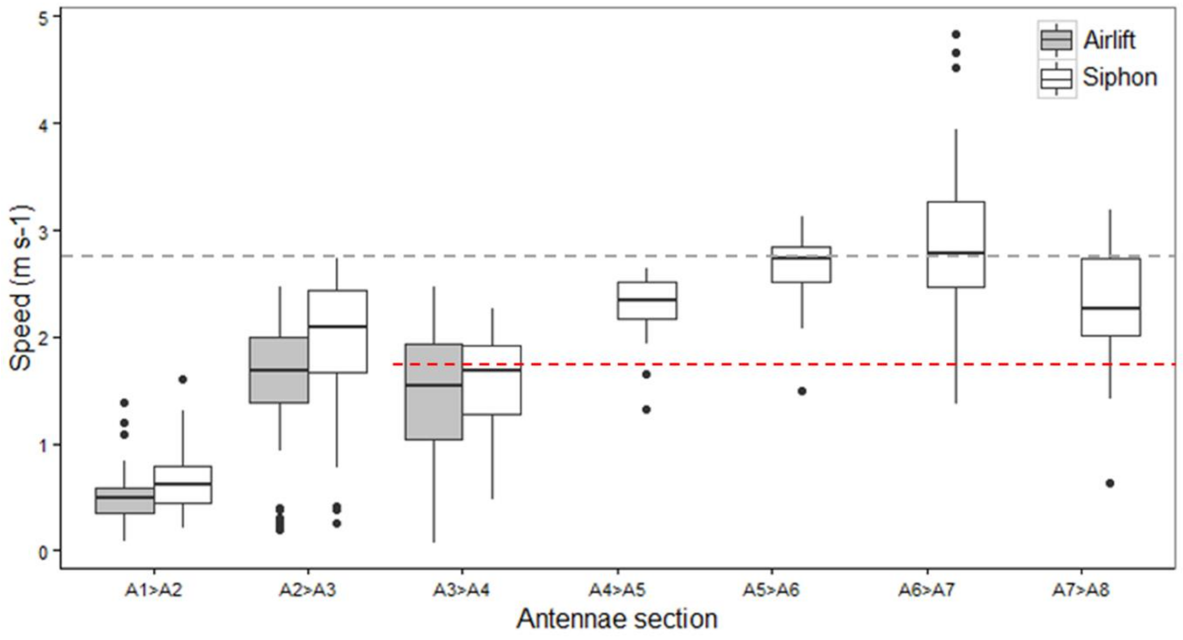

Figure 4. Speed (m s^{-1}) through each section of the airlift and siphon bypass (whiskers indicate range, midline indicates median, upper and lower limits of box indicate 75th and 25th percentiles, outliers [>1.5 times the interquartile range] indicated by black dots), dotted line indicates estimated water speed through each section of bypass.

3.5 Effect of different experimental designs on slip ratio

3.5.1 Slip ratio between bypasses and bypass sections

The siphon had significantly higher slip ratio (0.9 ± 0.2, 0.3 – 1.3) for vertically upward moving eels (A3>A4) than the airlift (0.6 ± 0.2, 0.0 – 1); (t-test; t = -8.10, df = 104, P <0.01), (Figure 5a). There was no significant correlation between eel length and slip ratio in this section of either bypass (Pearson product moment correlation, P >0.05).

The siphon bypass also included horizontal and vertically downward moving eels, thus slip ratio and the influence of gravity was also assessed. Slip ratio in the vertical upflow section (A3>A4; 0.9 ± 0.3, 0.3 – 1.3) was comparable to that in the horizontal section (A5>A6; 1 ± 0.1, 0.5 – 1.2) and the vertical downflow section (1.0 ± 0.2, 0.2 – 1.2); (KW-test; $X^2 = 0.76$, df = 2, P >0.05; Figure 5b). Again, there was no correlation between length and slip ratio in the horizontal or vertical downflow section of the siphon bypass (P >0.05; Pearson product moment correlation). There was no difference between slip ratio and different orientations of eels within each bypass (ANOVA; P >0.05).

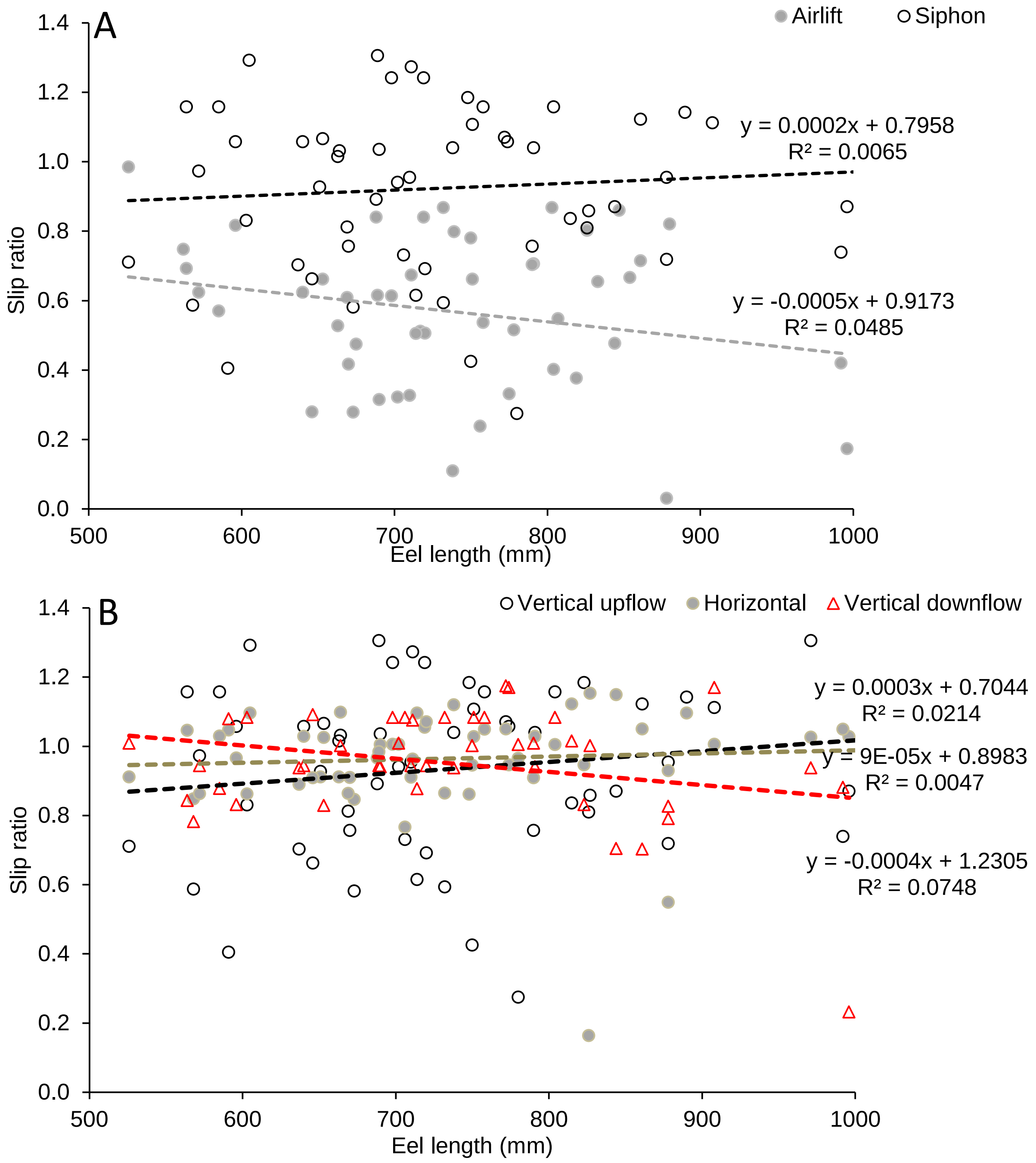

Figure 5. A) Slip ratio between the airlift and siphon bypass and B) between the horizontal and vertical sections of the siphon bypass. Colour of trendlines for data in each group corresponds to data points in that group. Intercept and R^2 values displayed.

3.5.2 Slip ratio at different flows and between years

Slip ratio of eels tested at the three flows in 2014 did not differ significantly (KW-test; X^2= 2.3325, df = 2, P = 0.3115) but in 2015 eels had a significantly higher slip ratio (0.6 ± 0.2, 0 – 1) compared to eels at the same entrance velocity in 2014 (0.3 ± 0.3, 0 – 0.7 m s^{-1}; Wilcox test; W = 132, P <0.05). There was no significant correlation between eel length and slip ratio in any of the flows in 2014

(Pearson product moment correlation, P > 0.05), and overall, eels in 2015 were significantly larger than those trialled in the previous study conducted in 2014 (Haro et al., 2016) (t = -2.3748, df = 92.853, P <0.05) but eye index was significantly smaller (t = 7.0691, df = 100.26, P <0.05).

3.6 Injury and mortality

All eels were alive, actively swimming and exhibited no external signs of injury or stress after the trials on the airlift and siphon bypasses. Latent mortality 48 h post-testing was zero, with no external evidence of developing injuries. Eels were released to the wild after the post-trial observation period.

4 Discussion

Addressing the issue of barriers to the downstream migration of *Anguilla* species is currently at the forefront of fish passage research. Types of barriers requiring remediation globally vary widely, warranting the need for bypass designs to be suitable for a broad range of installations. Results from eel bypass studies in the field have previously been inconclusive (Legault et al., 2003; Calles et al (2012) or reported variable results (Boubée and Williams, 2006; Gosset et al., 2005). Controlled flume conditions make it possible to quantify and better understand eel behaviour around bypasses, which aids in determining the optimum settings for efficient passage before installation in the field. In this study, bypass flows were generated in two different ways, but attraction, entrance and passage rates were comparable; eels entered both the airlift and siphon bypasses quickly (typically in less than 2 hours), and all eels that entered successfully passed, mostly in headfirst orientation and on the first attempt. There was no mortality or visible signs of injury on any eels that passed. Hence there were no physical deleterious effects on eel health or survival from the way flows were generated. Further, all metrics used to assess performance in this study were comparable to a previous airlift study (Haro et al., 2016), and demonstrate the repeatability of the approach and thus confidence in its potential real-world application.

Extensive delays to eels at structures have been observed (Piper et al., 2013), with searching behaviour at intakes (Brown et al., 2009; Behrmann-Godel and Eckmann, 2003) and rejection of passage through bar racks (Russon et al., 2010) being exhibited. These behaviours reduce the initial risk of eels being entrained into potentially hazardous intakes and provide an opportunity for them to find and enter safe downstream passage routes. Eels are known to actively search for a downstream passage route near the bottom of the water column in forebays of structures such as hydropower stations (Brown et al., 2009; Gosset et al., 2005) and navigate by following the walls and floor (Russon and Kemp, 2011); consequently bypass location will influence the ability of eels to find the bypass entrance, i.e. attraction efficiency.

Flow is one of the main drivers for the downstream spawning migration (Stein et al., 2016), and thus providing an attractive flow at the entrance to the bypass increases the likelihood of eels successfully locating the entrance and subsequently entering. Understanding the swimming capabilities of emigrating fishes is essential to ensure that fish that enter bypasses eventually encounter water velocities that exceed their burst swimming speed, hence preventing them from swimming upstream against bypass flow and avoiding entrainment into a bypass (see Nestler et al., 2008). As most eels entered the first time they approached either bypass, and no eels exited either bypass after passing the first antenna, this would indicate that the flows and associated velocity gradients trialled in this study are attractive to eels. This is unlike findings from Piper et al., (2015) who reported avoidance of constricted, accelerating flow and changes in behaviour under this condition by 95% of eels ($n = 35$), but at lower entrance velocities (range 0.14 to 0.67 m s^{-1}) than at the entrance to the bypasses trialled in this study. In the field, bypass operation should coincide with other environmental factors known to be favourable to migrating eels such as lunar cycle and time of year (Tesch, 2003) to maximise downstream passage efficiency.

Eel orientation when entering the bypass did not affect speed through either bypass nor did it result in any eels reversing course after entering the pipe. In terms of bypass efficiency, it is felt that the focus should be on ensuring that fish cannot escape from the bypass once entrained, provided chosen flow settings result in safe passage for all test subjects, as found in the present study. Based on speed of movement through the bypasses, it is unlikely eels attempted to leave the pass in an upstream direction and thus eel energy reserves would not be depleted during passage. Eels readily passed through longer lengths of pipework during the siphon experiment; this is encouraging as real-world bypass installations may require longer lengths of pipe.

Faster movement through the siphon bypass than the airlift bypass (A1>A2 and A2>A3) may indicate that either flows experienced in the siphon are easier to navigate or eels are more reluctant to move through flows created by the airlift, potentially due to reaction of eels to the injection of air (or associated sound/pressure changes) at the manifold. As speed was most variable between A2>A3 and A6>A7 in the siphon, this may indicate that eels were reluctant to move around bends during passage. Nonetheless, slip ratios were comparable between the vertical upward, horizontal and vertical downward section of the siphon, demonstrating movement through the entire siphon bypass was uniform. Further, slip ratios were comparable between the three flows tested during the 2014 airlift bypass trial. Speed of eels through the downstream section of the siphon was significantly lower than the previous two sections; this is difficult to explain. However, long or straight sections of pipework may affect speed and additional studies may help understand this relationship to ensure safe exit from the bypass. Regardless, tested in-pipe velocities within sections A4>>A8 (approximately 1.8 m s^{-1}) prevented eels from reversing course and escaping back upstream through the siphon.

As sexual dimorphism exists in eels (Oliviera and McCleave, 2002) and most migratory eels often move simultaneously in response to an increase in rainfall and flow (Haro, 2003), mature eels of a range of sizes will require a downstream passage solution at similar times. As there was no influence of sample size or eel size on the attraction time, passage speed or slip ratio of either bypass, this indicates that both bypasses were attractive to and suitable for larger migratory eels with a range of biological features, regardless of number of eels in the forebay; these results are favourable in terms of maximising passage in real-world scenarios. Because only large female eels were tested, passage behaviours, through-pipe speeds, and slip ratios could be different for smaller male eels; additional testing of smaller male eels may be warranted. Further, the findings are likely applicable to other anguillid species as both American and European eel species have been reported to have similar swimming abilities and behaviour (Clough et al., 2002; Solomon and Beach, 2004).

As the method of flow generation did not influence bypass efficiency, this broadens the real-world applicability of the findings presented here; airlift and siphon bypasses have differing installation and operational requirements. For example, siphon bypasses require the water level downstream of the barrier to be lower than the upstream water level, but this is not a prerequisite of airlift bypass operation, so such a measure may be suitable at pumping stations that transfer water to a higher level. Airlift bypasses require at least a 4 m riser pipe to generate the entrance velocity trialled in this investigation and thus the installation location must exceed this depth unless the bypass is excavated into the river bed. A limitation of airlifts is that they lift water a relatively short distance, 33.5 cm during this investigation, and thus an open channel sluiceway or collection device may be required with an airlift. A collection device may have problems with respect to debris loading and eels may need to be manually sorted from debris and transported downstream. Siphons do not require a water pump once they are operational, and fish are not subject to any pumping action (Bethune*,* 1997). Therefore, cost-effectiveness of each design (siphon or airlift) will depend on scale and characteristics of the site. If conservation of water is an important factor at a site, then the airlift might be a more cost-effective option than a siphon, since lifted water from an airlift can be recirculated back to a forebay or reservoir by gravity.

It is clear from previous research on this topic that the success of bypass systems for eels is not only affected by the design of the bypass, but also the nature of the site. As mentioned, variable results have been found in forebays of power stations, reservoirs and over spillways. Our experimental setting was limited to approach velocities of 15 cm sec^{-1}; the question remains whether eels would locate airlift or siphon entrances and enter them under higher intake approach velocities (i.e. up to 1 or more m sec^{-1} in some hydroelectric forebays), or forebays that are larger or with higher competing intake flows. However, in field trials the airlift bypass has been shown to attract and pass significant numbers of downstream migrant eels at small water supply intakes with low approach velocities (e.g., 0.26 m^{-3} sec^{-1} flow, 0.03 m sec^{-1} approach velocity, Groton Public Utility, Connecticut, USA; S. Gephard, Connecticut Department of Energy and Environmental Protection, pers. comm.). Assuming siphons and airlifts can be scaled up in size and flow volume to agency design criteria for downstream bypasses (e.g., USFWS, 2017), they should be as functional as other gravity/pump flow or other bypass designs at larger forebay environments. Clearly, there is a need to conduct further evaluations of airlift and siphon bypasses at other sites with different forebay hydraulics.

Conclusion

The findings of this study support that an attractive bypass channel holds promise for providing a safe route for downstream migrating eels. It was determined that two bypasses with flows being generated by air injection and siphon design both performed comparably, with most eels being attracted to the bypasses and passing quickly on the first attempt. All eels that passed did so efficiently and safely, with no mortality or visible signs of injury upon exit. These findings and those in the previous study (Haro et al., 2016) add to the knowledge base for determining what an effective downstream route for eels is, of which there is currently a lack of knowledge despite the need globally to solve this problem. Further research into entrance velocities, size and shape are required along with field studies to demonstrate real-world effectiveness, especially in scenarios where intakes generate competing flows. Regardless, the novel findings presented are encouraging for improving downstream passage for Anguillid species.

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