Effect of substrate roughness, slope, and body size on climbing behavior and performance of juvenile American eels (*Anguilla rostrata*)

A Masters Project Presented

by

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Abstract

The effect of ramp slope and substrate grain size on the passage of juvenile American Eel (*Anguilla rostrata*) over indoor ramps was tested from May – August 2016. Two size classes of fish (300 glass eels 50 – 70 mm and 300 elvers 90-114 mm), five substrates varying in coarseness (Substrate 1: 0.18-0.25 mm grain size, Substrate 2: 0.25-0.60 mm grain size, Substrate 3; 0.60-1.00 mm grain size, Substrate 4: 1.00 – 2.00 mm grain size, Substrate 5: 2.00-4.00 mm grain size), and three ramp slopes (25, 35 and 45 degrees) were explored. Individual fish were placed at the bottom of a ramp and given 30 minutes to ascend 0.5 m. Movements over the substrate were recorded with video footage and digitized. Fish length, fish weight, water temperature, and days the fish were held in captivity before being tested were also recorded and analyzed. Results indicated that substrate had a highly significant effect on glass and elver climbing performance, and slope had an effect on elver performance but not glass eel performance. The roughest substrate yielded the highest proportion of eels ascending the entire length of the ramp and the highest climbing speed in each parameter category. Further testing with more grain sizes and longer ramp lengths are required, and mass manufacturing processes for this substrate need to be explored.

Introduction

Populations of Atlantic freshwater eels (Genus *Anguilla*) have been declining rapidly since the 1980s (*ICES Report of the Workshop on Eel Stocking (WKSTOCKEEL)* 2016; Haro et al. 2000; Richkus and Whalen 2000). In some areas the decline has resulted in sub-populations at 1% of historical records (Verrault et al. 2012). For example, at the Moses Saunders Dam on the St. Lawrence River, the average eel count was 890,000 in 1985, declining to 4000 in the early 2000s (McGrath et al. 2003). Four major potential causes of population decline are:

anthropogenic chemical contamination, changes in ocean currents and temperatures, commercial fishing and anthropogenic habitat modifications (Castonguay 2015; Verrault et al. 2012). The major obstacles to both upstream and downstream migration of anguillid eels are dams and similar structures (Hitt et al. 2012), and various case studies have shown that dams are a major part of anthropogenic habitat modification. A historical study of the Richelieu River in Canada showed a dramatic decrease in silver eel landings (72.9 to 4.7 metric tonnes) and an increase in eel size that coincided with the building of two crib dams on the river (Verdon et al. 2002) since barriers and passage ways are typically size selective favoring larger fish. Obstacles to migration also may have secondary effects, such as contamination, disease and predation risk (Haro et al. 2000).

The life cycle of the eel starts with the adults migrating out to sea from the inland areas of the east coast during early fall. Once downstream and past estuaries the adult eels reach the Atlantic and head towards the Sargasso Sea where American eels all congregate and spawn. Eggs hatch into *leptocephali*, larvae that then start migrating towards the mainland (Regan Tate et al. 1922; Tesch 2003). *Leptocephali* metamorphose into unpigmented *glass eels* by the time they reach coastal areas. Glass eels are roughly 50 to 80 mm in length and ascend freshwater streams and rivers, undergoing further growth and recruitment of pigment. Larger pigmented glass eels may be termed *elvers,* but there is no definitive age or size range for elvers. Eventually elvers enter the primary *yellow eel* growth phase, reaching sizes of approximately 200 to 1000 mm TL. At maturity, yellow-phase eels transform to the adult silver phase and migrate downstream to the ocean and the Sargasso spawning area

Upstream passage of glass eels and elvers can be facilitated with the use of eel ramp passes (Solomon and Beach 2004). Typical technical fishways often do not allow for efficient passage of small anguilliform fishes like glass eels and elvers as they are designed for stronger-swimming carangiform and subcarangiform fishes (Gillis 1996). Additionally, juvenile eels do not require full submergence and can climb wetted surfaces. Eel ramp passes are typically sited in areas that have natural concentrations of glass eels and elvers (Larnier 2002). These passes usually consist of a ramp structure that can be constructed of wood, metal, or concrete at slopes between 15 and 45 degrees (Knights and White 1998). The ramp entrance is typically submerged in water with a supplementary attraction flow that allows the juveniles to locate the ladder. Ramp pass exits can open either directly upstream or can lead to a trap where the juveniles are collected, counted and then released upstream. Ramps are usually lined with a rough substrate such as bristles, studs, gravel, geotextiles, fibrous material, plastic molded material, or other structures to enhance climbing ability of eels (Knights and White 1998; Tesch 2003). Several climbing substrates have been purpose-designed for eel passes (e.g. bristle substrate, FISH-PASS; vertical cylinder substrate, Milieu, Inc.; stud/boss substrate, Berry and Escott Engineering), but many are simply manufactured materials intended for other purposes (e.g., geotextiles, foundation drain, or even trawl netting).

Little research has been conducted to determine the effect of degree of roughness, shape of roughening elements, ramp slope, or ramp flow on glass eel and elver climbing efficiency. Jellyman et al. (2016) evaluated optimal ramp conditions for *Anguilla australis* elvers <155 mm TL for three substrates: plastic, sand/gravel with a grain size between 2-15 mm, and Miradrain© (a plastic molded product) at ramp slopes of 30, 50, and 70 degrees. The ramps were laterally tilted at 10 degrees to create a wetted margin and variety of depths. The final recommendations were to maintain lower ramp angles and use Miradrain© since this provided increased passage performance.

Other experiments explored the passage efficacy of crump weirs covered in various types of substrates. James et al. (2015) tested European eels (*Anguilla anguilla)* with vertically oriented bristle substrate in an experimental flume. Flow was constant but downstream water depth was varied. High velocity and turbulence (Liao 2007) were found to be detrimental to the passage of smaller eels and bristle passes were determined to be an effective way to improve passage in structures where high velocity regimes are inevitable. Vowles (2015) also studied crump weirs covered in dual density studs compared to no substrate under uniform flow. It was determined that the substrate increased passage from 0% to 67% and a greater percentage of total glass eels utilized the smaller studs (59%).

Size of eels, water temperature, and time of day/season may also affect climbing ability and ramp pass performance. (Tesch 2003; Solomon and Beach 2004; Linton et al. 2006). Therefore, current designs of eel ramp passes and substrates may not be optimized for maximum passage performance, and may be both size-selective and inefficient (Verdon et al. 2002).

This study investigated the primary effects of ramp pass roughness (sand/gravel substrate with 0.13 mm to 4.00 mm diameter grain size), and slope (25 to 45 degrees from horizontal) on climbing performance of American eel glass eels and elvers (5-14 mm TL) under controlled laboratory conditions. The effect of fish size and weight on climbing performance was also investigated, as well as covariate effects of water temperature and number of days in captivity which varied during experimental trials. We quantified passage performance as absolute distance, time to ascent and rate of ascent, and number of attempts during 30 min trials.

Methods

Fish Collection and Holding

Glass eels (5cm – 7 cm; pigmentation stage 2-6 (Haro and Krueger 1988) were collected between 10 May and 17 June 2016 at the Fishing Brook eel ramp trap in Old Saybrook, Connecticut, USA (N 41° 17' 46.57", W 72 ° 23' 41.44"). Elvers (9mm-14mm; at least age 2+) were collected between 7 July and 22 August 2016 at the Holyoke Dam eel ramp traps in Holyoke Dam, Massachusetts, USA (N 42° 12' 42.20", W 72° 36' 9.63"). Glass eels and elvers were collected every 1 to 3 weeks and were transported in aerated containers back to the testing facility at the U.S. Geological Survey S.O. Conte Anadromous Fish Research Laboratory, Turners Falls, Massachusetts, where they were kept in holding tanks supplied with ambient water from the Connecticut River. Most eels were held unfed but glass eels held longer than 2 weeks were fed raw fish liver.

Experimental Apparatus

A tilting ramp test structure frame (*Figure 1*) was fabricated from wood and plywood. Five formed aluminum sheet test channels were attached to the tilting ramp frame. Test channels were 0.61 m wide by 0.30 m long and had v-shaped floors with lateral angles of 5 degrees to keep flow within the center of the channel, and create a uniform wetted margin of varying flow depth between the center of the channel and the channel wall. River gravel was collected and sieved into five categories of grain sizes. The test channel floors were coated with epoxy and gravel from each grain size category was glued on to each ramp. This resulted in five test channels with substrates of varying floor roughness ranging from smooth to coarse: Substrate 1: 0.18-0.25 mm grain size, Substrate 2: 0.25-0.60 mm grain size, Substrate 3; 0.60-1.00 mm grain size, Substrate 4: 1.00 – 2.00 mm grain size, Substrate 5: 2.00-4.00 mm grain size. Water was supplied to each test channel from a head tank connected to a five pipe manifold. Valves on each pipe regulated water flow down the center of each test channel (approximately 0.60 L/min). Water exited the test channel through a finely perforated screen at the downstream end of the channel; an adjustable external standpipe regulated tailwater level at the bottom of all test channels. The tilting ramp frame could be pivoted to adjust slope of all five test channels simultaneously at 25°, 35°, and 45°.

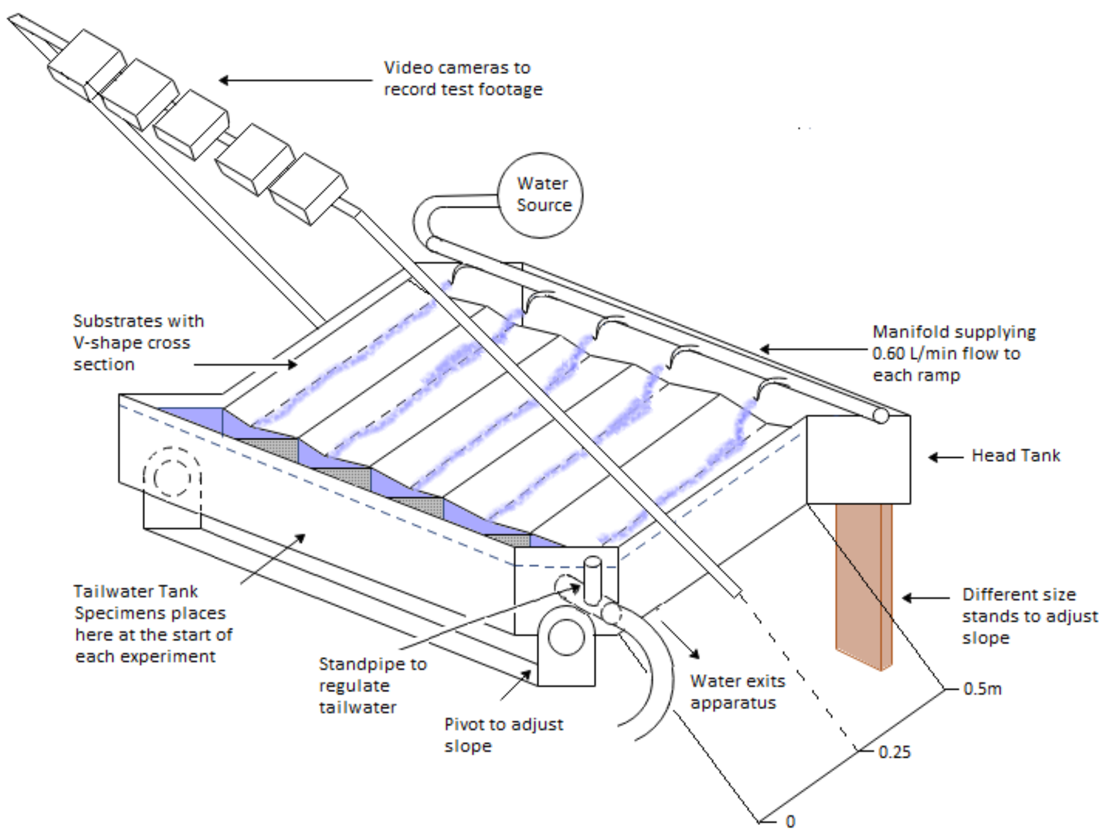

Figure 1: Tilting ramp structure used to conduct slope and substrate testing.

Experimental Protocol

Tests were conducted between 11 May and 16 August 2016. Because juvenile eel typically climb at night (Lowe 1952), and cannot see red light well (Beatty 1975), the tests were run in a dark room with dim overhead red lights (75-150 lux at the ramp surface) to aid in observing and recording eel movements. The combination of five substrates and three slopes resulted in fifteen different possible treatments. 40 fish were run for each treatment: 20 glass eels and 20 elvers. In total 600 fish were tested, with each fish being used for one single test run. Each test began with one fish placed in the downstream end of a test channel that had approximately 1 cm of tailwater depth, and allowed to volitionally ascend the channel. Trials were ended after 30 min or when fish reached the top of the 0.5 m long test channel. Movements of eels on the test channel were recorded using digital video (AXIS model Q1604 cameras, 720p resolution, iSpy PC-based recording software). At the end of the test, the fish was removed from the test channel and anaesthetized in a solution of MS222, measured (nearest mm) and weighed (nearest 0.001 g). Eels were released to the lower Connecticut River after testing.

Data Analysis

Digital video recordings of eels ascending ramps were processed using video distance and time measurement software (Tracker; Open Source Physics). Positions (x and y coordinates of position of the head, measured every 5 s to the nearest mm for the 30 min observation period) and time (nearest second) were digitized and entered into an MS Excel spreadsheet, and tracks of individual fish (distance moved along the vertical axis of the ramp channel over time) were generated. Track data were then analyzed to derive the following metrics, with the time when the eel was first placed in the test channel set as 0 s *(Figure 2)*:

Attempt: a climbing event where the entire body of the eel moved above the level of the tailwater. Movement back down to the tailwater and reascent above the tailwater was classified as a separate attempt. Movement to the top of the ramp channel without returning to the tailwater was classified as a single attempt.

$N_{attempt}$: Number of attempts during the entire 30 min trial.

D_{max}: Maximum distance ascended by specimen. This was 0.5 m for when the eel reached the top of the substrate during the test.

T_{start}: Time at which the eel started ascending the ramp.

$T_{attempt}$: Time at which the eel started to ascend the attempt at which it reached **D_{max}**

T_{max}: Time at which the eel reached the maximum distance climbed during the 30 min trial. T_{max} was set to 1800 seconds in trials where the fish did not successfully reach the top.

Speed: Climbing speed of the test specimen calculated as **$D_{max}/(T_{max}-T_{attempt})$**

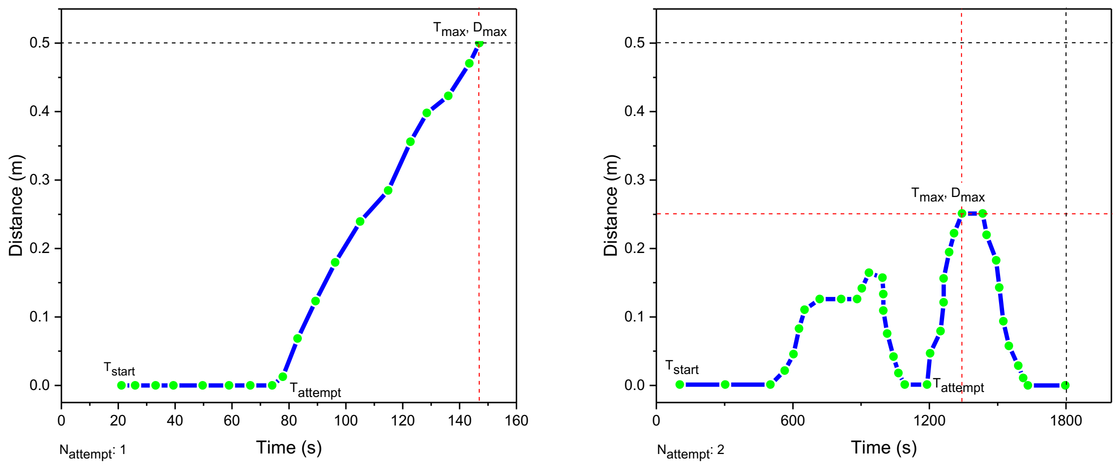

Figure 2 Sample tracks of eel ascent of a substrate. Left: Ascending eel rapidly reaches the top of the 0.5 m long ramp in a single attempt. Right: Ascending eel makes two separate attempts; D_{max} was established on the second attempt, which had the greatest distance of ascent. Black dotted lines depict the maximum distance of 0.5 m and maximum time of 1800 s or 30 min. Red dotted lines indicate the times and distances where D_{max} and T_{max} were established for each test. Note that x-axis scales are different because the tests ended at 30 minutes or when the fish reached the 0.5 m mark, whichever event occurred first.

Statistical Analysis

Data from the MS Excel spreadsheet were imported to Origin2017 (OriginLab Corp.) for analysis. Cox proportional hazards regression (Cox 1972) was conducted with T_{max}, D_{max}, and T_{start} as the dependent variables, and substrate, slope, fish length, fish weight, water temperature, and days in captivity as independent variables. T_{max} values of 1800 s were censored because eels could potentially ascend the ramp if the test was run longer than 1800 s, and D_{max} values of 0.5 m were censored because eel could potentially have kept climbing if the maximum distance of ascent was not limited to 0.5 m. An interaction term (Length*Weight) was added to the model since Length and Weight are correlated. A backward-elimination stepwise regression was performed to extract significant variables. Multiple linear regression was performed on Speed data with the same interaction term for Length and Weight. A backward-elimination step wise regression was again used for Speed to determine significant variables.

Results

The testing conditions and parameters are summarized in *Table 1*. Glass eel total length ranged between 50-69 mm and elvers between 90-147 mm. Glass eels had a higher length/weight ratio than elvers *(Figure 3)*. Glass eels and elvers were collected at two different locations with differing age/size class structures, so no eels between 70-90 mm were tested. Of the 301 glass eels tested, 49% ascended to the top of the 0.5 m ramp; of the 298 elvers tested, 83% ascended to the top.

Tables 2a (glass eels) and *2b* (elvers) display statistics for attempts in percentage. For conditions where 0% of the fish made 0 attempts it indicates that all the fish attempted to climb even if they did not reach the 0.5m mark. For example, at the 25 degree slope on Substrate 5 all fish tested attempted with 82% making at least one attempt, 14% making between two and four attempts and 5% making more than 4 attempts. Fish that made one attempt only typically reached the 0.5m mark in that attempt.

The results of the Cox regression and multiple linear regression are provided in *Tables 3a* (glass eels) and *3b* (elvers). For non-significant variables, the estimate and significance from the last step before the variable was removed in the backward elimination step wise process is provided. Significant variables are those with p and t values lower than 0.05.

Glass Eels:

The $N_{attempts}$ table (*Table 2a*) indicates that glass eels exhibited a lower proportion of climbing attempts on smoother substrates and steeper slopes. Additionally, very few fish made more than four attempts, and the highest number of average attempts per fish occurred on

Substrate 3. The reverse stepwise elimination process yielded significant variables that differed from a regression performed on a model with all the variables. For glass eels, the effect of slope was significant for T_{start} and Speed (*Table 3a*; Cox regression, $p < 0.024$; multiple linear regression, $t < 0.002$). The effect of substrate was highly significant for all the dependent variables, D_{max}, T_{start}, T_{max}, and Speed (Cox Regression, $p < 0.001$, multiple linear regression, $t < 0.001$). The effect of length of glass eels was not significant for any of the dependent variables although the effect of weight was significant for T_{start} (Cox regression, $p< 0.002$), T_{max} (Cox regression, $p< 0.001$), and highly significant for Speed (multiple linear regression, $p< 0.001$). Like length, water temperature was not significant for any dependent variable. Similar to weight, the number of days glass eels were held captive before being used for testing was significant for T_{start} (Cox regression, $p< 0.002$), T_{max} (Cox regression, $p< 0.002$), and highly significant for Speed (multiple linear regression, $p< 0.001$) as well. Overall, substrate roughness generally had a larger effect on performance than ramp slope. This is also depicted in the box plots; for D_{max} the difference between substrates for glass eels can be seen by the sharp change in performance on Substrate 3 which is the only substrate where slope seemed to have an effect *(Figure 4a*). Glass eels performed similarly on each slope but the speed increased for rougher substrates *(Figure 4b).*

Elvers:

Similar to glass eels, the $N_{attempts}$ table (*Table 2b*) indicates that elvers exhibited a lower proportion of climbing attempts on smoother substrates and steeper slopes. The greatest percentage of elvers that made zero attempts to climb occurred at the steepest slope of 45 degrees on the smoother Substrates 1, 2 and 3. Unlike the glass eels analysis the reverse step wise elimination process yielded the same significant variables as those from a regression performed on a model with all the variables. For elvers, slope was highly significant for all four dependent variables D_{max}, T_{start}, T_{max} and Speed (*Table 3b*; Cox Regression, p< 0.001, multiple linear regression t< 0.001). Similarly, Substrate was also highly significant for D_{max}, T_{start}, T_{max}, and Speed (Cox regression, p< 0.001; multiple linear regression t< 0.001). Length and Weight were not significant for any of the dependent variables. The temperature of the water was significant for only Speed (multiple linear regression t<0.052). Captivity was significant for T_{start} and T_{max} (Cox regression; p<0.005, p<0.002 respectively). The regression results indicate that both substrate and slope affected elver performance. As depicted in the box plots almost all the elvers were successful on the rougher substrates for all the slopes, and on the smoother substrates for lower slopes. The range of performance got wider on smoother substrates with higher slopes *(Figure 4a*). Like glass eels, elvers generally climbed faster on lower slopes for all substrates, although their climbing speeds are higher than glass eels for each category. *(Figure 4b)*. Elvers performed better on lower slopes and rougher substrates.

Table 1: Summary of test eel numbers, sizes and weights, test conditions, and frequency of attempts. "No Attempts" indicates the number of test fish that did not make any attempts to ascend the ramp. "Incompleted Attempts" refers to number of fish that made an attempt but did not achieve a D_{max} of 0.5 m to the top of the ramp. "Completed Attempts" refers to specimens that made an attempt and achieved a D_{max} of 0.5 m.

Size Class	Size (mm)	Weight (g)	Temperature Range (C°)	Test Dates	Specimens Tested	No Attempts	Incompleted Attempts	Completed Attempts
Glass	50 - 69	0.038 - 0.280	12 - 23	11th May - 17th Jun	301	115 (38%)	38 (12%)	148 (49%)
Eel	90 - 147	0.6 - 3.6	22 - 28	7th Jul - 23rd Aug	298	27 (9%)	20 (7%)	251 83%)

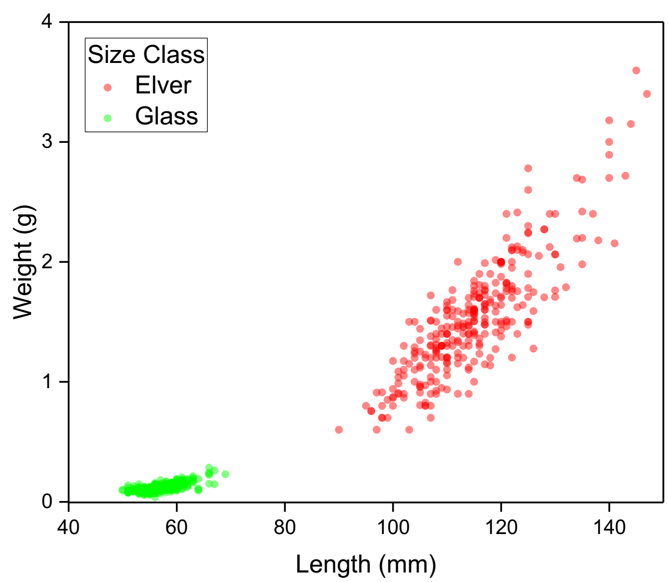

Figure 3 Length and weight relationship for tested glass eels and elvers.

Table 2a: Number of attempts of glass eels, expressed as a percentage of total attempts for each substrate within each slope condition. Fish that had only one attempt typically ascended to the top of the ramp on that attempt.

		Ramp Slope											
		25°				35°				45°			
	$N_{attempt}$ %	**0**	**1***	**2 - 4**	**>4**	**0**	**1***	**2 - 4**	**>4**	**0**	**1***	**2 - 4**	**>4**
Substrate Roughness	*Substrate 5 (rough)*	0	82	14	5	0	90	10	0	0	86	14	0
	Substrate 4	0	86	9	5	0	95	5	0	5	77	14	5
	Substrate 3	13	71	4	13	25	70	5	0	5	68	14	14
	Substrate 2	84	16	0	0	80	20	0	0	95	5	0	0
	Substrate 1 (smooth)	91	9	0	0	80	20	0	0	95	5	0	0

Table 2b: Number of attempts of elvers, expressed as a percentage of total attempts for each substrate within each slope condition. Fish that had only one attempt typically ascended to the top of the ramp on that attempt.

Elver		Ramp Slope											
		25°				35°				45°			
	$N_{attempt}$ %	**0**	**1**	**2 - 4**	**>4**	**0**	**1**	**2 - 4**	**>4**	**0**	**1**	**2 - 4**	**>4**
Substrate Roughness	*Substrate 5 (rough)*	0	89	11	0	0	86	14	0	0	100	0	0
	Substrate 4	0	89	11	0	0	95	5	0	9	77	14	0
	Substrate 3	0	71	24	5	19	73	8	0	30	60	10	0
	Substrate 2	0	71	29	0	25	75	0	0	43	52	5	0
	Substrate 1 (smooth)	9	73	18	0	5	86	10	0	30	65	5	0

*Table 3a: Results of reverse stepwise Cox proportional hazard regression on D_{max}, T_{start} and T_{max} for Glass Eels where * and ** denote significant (P <0.05) and highly significant (p <0.001) relationships, respectively. Results for reverse stepwise linear multiple linear regression on Speed for Elvers where * and ** denote significant (Prob|t|<0.05) and highly significant (Prob|t|<0.001) respectively. The values for each non-significant independent variable are the last estimate before they were removed from the model. The significant variables are included in the final model after stepwise regression.*

Glass Eels

Dependent Variable	**D_{max}(m)**		**T_{start}(s)**		**T_{max}(s)**		**Speed (mm/s)**	
Independent Variable	Estimate	Pr > ChiSq	Estimate	Pr > ChiSq	Estimate	Pr > ChiSq	Value	Prob>|t|
Slope (25 35 45)	-0.001	0.928	-0.022	**0.024***	-0.015	0.1046	-0.047	**0.002***
Substrate (1-5)	-1.007	**<0.001****	0.949	**<0.001****	0.853	**<0.001****	1.420	**<0.001****
Length (mm)	-0.039	0.078	0.008	0.813	0.032	0.6419	0.024	0.814
Weight (g)	-0.038	0.084	6.28	**0.002***	6.780	**0.001***	15.071	**<0.001****
Water temp (°C)	-0.009	0.738	-0.009	0.790	-0.0301	0.299	0.031	0.4781
Captivity (days)	0.009	0.406	-0.021	**0.028***	-0.019	**0.059***	-0.068	**<0.001****
Interaction (Length Weight)*	-0.334	0.556	-0.251	0.604	-0.5706	0.224	-0.633	0.418

*Table 3b: Table 3a: Results of reverse stepwise Cox proportional hazard regression on D_{max}, T_{start} and T_{max} for Elvers where * and ** denote significant (P <0.05) and highly significant (p <0.001) relationships, respectively. Results for reverse stepwise linear multiple linear regression on Speed for Elvers where * and ** denote significant (Prob|t|<0.05) and highly significant (Prob|t|<0.001) respectively. The values for each non-significant independent variable are the last estimate before they were removed from the model. The significant variables are included in the final model after stepwise regression.*

Elver

Dependent Variable	**D_{max}(m)**		**T_{start}(s)**		**T_{max}(s)**		**Speed (mm/s)**	
Independent Variable	Estimate	Pr > ChiSq	Estimate	Pr > ChiSq	Estimate	Pr > ChiSq	Value	Prob>|t|
Slope (25 35 45)	0.071	**<0.001*** **	-0.050	**<0.001*** **	-0.044	**<0.001*** **	-0.247	**<0.001*** **
Substrate (1-5)	-0.426	**<0.001*** **	0.260	**<0.001*** **	0.303	**<0.001*** **	1.180	**<0.001*** **
Length (mm)	0.013	0.366	0.002	0.732	0.0006	0.916	0.010	0.923
Weight (g)	-0.273	0.894	1.520	0.218	1.871	0.114	-0.698	0.327
Water Temp (°C)	-0.144	0.131	-0.015	0.783	-0.060	0.235	-0.573	**0.052***
Captivity (days)	-0.0828	0.060	0.047	**0.005***	0.044	**0.001***	0.104	0.248
Interaction (Length Weight)*	0.010	0.502	-0.014	0.170	-0.016	0.082	0.031	0.543

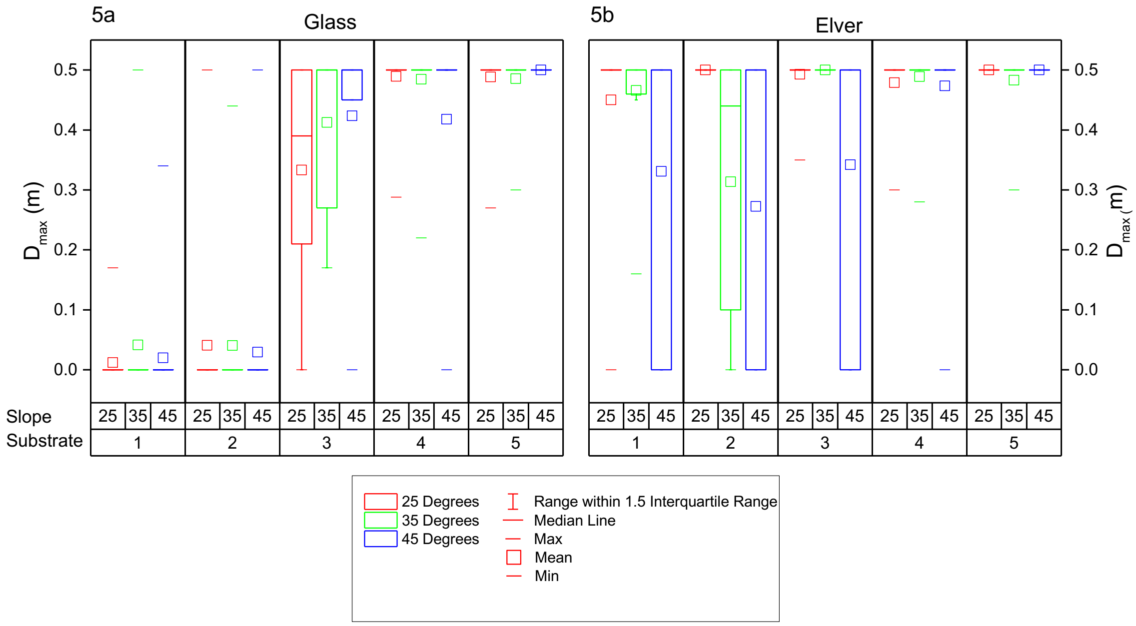

Figure 4 Box plots for D_{max} for Glass Eels (4a) and Elvers 4b)

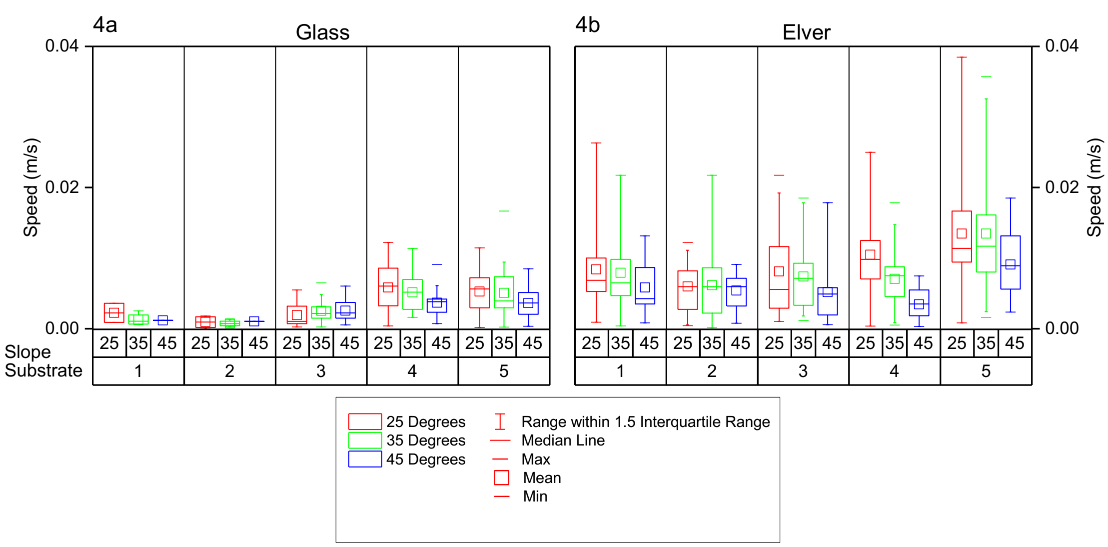

Figure 5 Box plots for Speed for Glass Eels (5a) and Elvers (5b)

Discussion

Climbing Behavior

Both glass eels and elvers exhibited two dominant modes of climbing behavior based on the coarseness of substrate and size of eel: "surface tension" climbing and "push off" climbing. It appeared that most fish used a combination of the two behaviors. For smaller eels, on fine wet surfaces body weight is low enough to use surface tension to adhere to even vertical walls. This behavior has also been observed in eels in the wild (Jellyman 1977). Forward locomotion is then facilitated by brief extension of the anterior part of the body and subsequent retraction of the posterior part of the body in an undulatory motion (Gillis 1998). The other method of climbing – push off climbing- involves using friction to push the eel's body off of larger protruding grains in the substrate while adapting their bodies to the substrate contours. During testing, it appeared that on smoother substrates the eels used primarily surface tension as a mode of climbing since there were no protruding substrate elements to push off from. Surface tension climbing was not as dominant on the rougher substrates because it required the entire body of the fish to be in contact with the substrate (Baker Boubee 2006), which was difficult for fish to accomplish on the uneven terrain of the rougher substrates. On these rougher substrates, the change in climbing behavior was evidenced by a change in body kinematics where both glass eels and elvers conformed their bodies to the substrate grain topography, roughly matching the grain orientation as they snaked their way up the ramp, rather than propelling their bodies by regular sinusoidal waves as in surface tension climbing (*Figure 5*.).

Behavior of glass eels showed a clear demarcation where performance levels changed based on the slope and substrate. For the smooth Substrates 1 and 2, where surface tension climbing dominates, few glass eels were able to start ascending the ramps at all regardless of slope, even when they repeatedly explored the wetted substrate near the bottom of the ramp.

Climbing performance shifted dramatically on Substrate 3, with more fish reaching the 0.5 m mark as compared to the two smoother slopes. However on Substrate 3 a greater portion of glass eels ascend on steeper slopes rather than on the lower slope as was expected, because the other behavior impacting factors such as temperature and days in captivity are not taken into account as they were in the Cox Survival Analysis. Overall, compared to the three smoother substrates, glass eels were faster and more successful at ascending the 0.5 m mark on the two rougher substrates regardless of slope, using primarily push off climbing. It was observed that push off climbing also allowed the fish to rest on the protruding grains of the rougher substrates with little effort without being swept back down by the flowing water. Because of this fatigue was less of a hindrance during climbing. With regard to fatigue, another drawback of surface tension climbing on the smoother substrates was the amount of energy required to start the climb. When first ascending smoother surfaces, it was noted that the test specimens employed burst swimming, which allowed them to generate enough momentum to leave the tailwater and leap on to the ramp, adhere with surface tension, and then start the sinusoidal motion for the ascent. However, on rougher substrates eels were observed to leave the water by working their bodies amongst the grains and starting their ascent. These observations indicate that initially, surface tension climbing behavior may be less efficient than push off climbing behavior.

Figure 5: Images of elvers ascending climbing substrates. Left panel: surface tension climbing on a smoother substrate (Substrate 2), with clear sinusoidal propulsion. Right panel: push off climbing on the coarser substrate (Substrate 5). Note irregular bends in the body used over the coarser substrate, conforming to gaps between substrate grains, typical of push-off climbing.

Additional tests conducted during summer 2017 with glass eels on smooth aluminum ramps confirmed they could not ascend these very smooth surfaces. Glass eels were also qualitatively tested with a substrate of grain sizes ranging approximately 3.00 – 6.00 mm, slightly larger than those on Substrate 5. Climbing speed of glass eels on this very coarse substrate declined compared to Substrate 5 as the test specimens appeared to find it difficult to navigate the deeper crevices and larger protruding grains. Therefore, theoretically the optimal climbing parameters for glass eels are substrates with grain sizes larger than 1.00 mm (maximum grain size for Substrate 3) and smaller than 4.00 mm (maximum grain size for Substrate 5). However, a quantitative analysis of larger grain size substrate performance for eels larger than glass eels needs to be conducted. Additionally, for the lower grain size limit it is difficult to explain the reduced performance of glass eel climbing on Substrate 1 since there have been numerous accounts of glass eels ascending vertical concrete dam walls with similar roughness. It is hypothesized that these dam walls may have smoother grains that have been worn down by erosion over time, as well as algal growth that may contribute to an easier ascent. Further testing of this hypothesis is recommended as well. Because slope did not appear to affect D_{max} or T_{max} and most fish ascended the rough substrates even at the steepest tested slope of 45 degrees, no upper limit on slope can be established from these tests. However, it is important to note that slope has an effect on fish speed and so a steep slope on a long ramp would require a lengthy passage time.

Larger elvers tended to climb faster than smaller glass eels under the same circumstances. The Cox analysis results and the box plot indicate that unlike the glass eels performance that depends primarily on substrate rather than slope, elver performance is affected by both slope and substrate. Predictably, elvers climbed fastest and most fish reached the top of the ramp on Substrate 4 and 5 at the 25 degree slope. On smoother substrates it was hypothesized that larger body size would reduce performance as the eels would not have the option to push off and would have to use more energy to keep moving in order to hold up their larger body weight with surface tension. On these smoother substrates on lower slopes elvers were able to ascend but exhibited slower climbing speed, and on steeper slopes they ascended lower distances. This may be attributed to their higher weight which, as hypothesized, was more difficult to keep attached via surface tension at steeper slopes and forced them to slide back down. The effect of body weight was significant for glass eel climbing performance but not elver climbing performance. Since glass eel weight varied between 0.038 and 0.284 g it can be hypothesized that even a minute change in weight affects fish climbing ability whereas for the larger elvers small changes in weight may not have a large impact. Length however did not show any significant effect on climbing performance within each life history stage. This could be due to the fact that glass eels showed a greater variance in performance but had a small range in length (19mm), whereas elvers showed lower variance in performance with the majority of fish in that size class ascending the 0.5 m ramp, but had a larger range in length (57mm). Although the interaction term did not have an effect on either size class, the difference in climbing abilities between elvers and glass eels indicates that weight and length can affect performance when there is a larger range in size. Because 83% of elvers ascended the full length of the ramps, limiting parameters for optimal elver climbing conditions are not clear. It can be hypothesized that the elver results can be attributed to their larger size combined with the ramp length. The maximum distance of ascent of 0.5 m was only 5 times the average body length of the elvers tested. A longer test ramp may have enabled more accurate assessment of motivation and fatigue for larger elvers.

Water Flow

Due to the use of surface tension for climbing, especially for smaller eels that cannot withstand high water flow velocities without getting washed down a ramp, the importance of a low water velocity wetted margin is often highlighted in the construction of eel ramps (Jellyman 1977; Yasuda et al., 2004; Baker and Boubée, 2006). Eels seem to prefer substrates that create a larger boundary layer that disrupts water flow and allows eels to progress upstream along the edges of a channel (Jellyman 1977; Tesch 2013; Vowles et al. 2015). On rougher substrates, water flow spreads out over a larger area, reducing the velocity and providing a larger wetted margin. On smoother substrates, flow tends to concentrate in rivulets or a single stream that has a higher velocity, and the transition between wet and dry is more abrupt which reduces the wetted margin. It was observed that for smoother substrates at steep slopes the test subjects often made no attempts to climb. However, fish made climbing attempts on rougher substrates at lower slopes. Since without climbing and failing the test specimen should still be motivated to attempt, it is hypothesized that juvenile eels sense the nature of the flow running down the ramp while they are submerged in the bottom tank and are motivated to leave the water and locomote terrestrially accordingly.

Various other factors serve as cues to juvenile eel upstream migration including water temperature, salinity, discharge, tidal cycle and precipitation (Jellyman and Lambert 2003; Bult and Dekker 2007; Mouton 2011; Piper et al. 2012, Linton et al. 2006). Motivation to climb is an important factor that could have affected the results of this study. The effect of length of time in captivity was significant; in general, specimens held longer had lower performance. Because glass eels were held for longer periods, time in captivity affected their performance more. Compared to glass eels that were tested in the spring, water temperature was more significant for elvers as they were tested in late summer when there was a greater range in temperature.

Conclusions

The experimental ramp tests run using two juvenile eel class sizes – elver and glass eel – indicate that substrate choice is crucial for effective design of upstream passage structures for glass eels. Grain size has a dramatic effect on both the distance and speed of ascent of glass eels on a substrate covered ramp. A grain size of 2.00 mm – 4.00 mm appeared to maximize climbing performance, allowing for faster climbing to higher distances on the ramp. Although at various sites juvenile eels have been observed climbing smooth vertical concrete dams using mostly surface tension climbing, it was ascertained that push off climbing on a substrate with larger elements is likely more efficient than climbing on smooth concrete.

Slope also has an effect on elver climbing performance but has a smaller impact on glass eel climbing performance. Because commercial eel passes are typically installed at the steepest possible slope to reduce cost and space, it is recommended that eel passes be constructed with steeper slopes using substrate with appropriate grain size, since the substrate grain size choice is not constrained by cost or available space for a ramp.

Further tests are required to refine the optimal substrate grain size for both glass eels and elvers. Future research should be performed with longer ramps so that fatigue can be better measured as a variable. Fatigue is important for larger dams, or sites where resting areas on a ramp may be limited. Once ramp design parameters are ascertained, a rough substrate may also be combined with stud or vertical tube commercial substrates to accommodate a wider size range of eels. The development of such an optimized substrate created specifically for juvenile eels of all sizes would reduce size selectivity in eel passes and thus increase both numbers and efficiency of passage of eels at migratory barriers.

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