Efficiency of a dual density studded fish pass designed to mitigate for impeded
upstream passage of juvenile European eels (*Anguilla anguilla*) at a model Crump weir

**ABSTRACT**

This study demonstrated that juvenile (glass) eels utilised a specific substrate (eel tiles) to
circumvent a model Crump weir under an experimental setting. Upstream passage efficiency
was 0% and 67% for the unmodified (no studded eel tiles on the downstream face; control)
and modified (with studded eel tiles on the downstream face; treatment) setups, respectively,
and greater for a small (59%) compared to large (41%) stud configuration. Eels were active
and motivated to ascend the weir during both control and treatment setups. Approach and
attempt rates were elevated during the first few minutes of the treatment compared to control
trials. Eels were edge oriented under both setups, and ascended the weir through the tiles
during single burst swimming events (reaching estimated speeds of 68.5 cm s\(^{-1}\)). Eel tiles may
provide a cost effective solution for mitigating impacts of anthropogenic barriers to juvenile
eel migration. Further research is required to determine passage efficiencies under higher
flows, for a greater size range of eel, and for other migratory anguilliform fish (e.g. lamprey,
*Lampretra* spp. and *Petromyzon marinus* L.). The performance of eel tiles should be
validated through robust field studies.

**KEYWORDS**: Barrier, behaviour, eel ladder, fish passage, flume, migration.

**Introduction**

The European eel, *Anguilla anguilla* (L.) is a species of high conservation concern due to a
dramatic decline in recruitment (e.g. greater than 90% in some catchments) throughout its
range over the last *ca.* 30 years (Dekker 2003). Adult eels migrate from rivers to oceanic
spawning grounds, thought to be in the Sargasso Sea, while the larval life-stage (leptocephali)
utilise ocean currents to return to continental waters (Tesch 2003). As they develop into “glass eels” they move through estuaries predominately by Selective Tidal Stream Transport (McCleave & Kleckner 1982; Beaulaton & Castelnaud 2005), and embark on active upstream migration in rivers as they metamorphose into the pigmented “elver” life-stage (Chadwick et al. 2007). Anthropogenic barriers (e.g. dams, weirs, sluices, culverts) can prevent or limit juvenile eel upstream migration in freshwater, restricting access to suitable rearing habitat and contributing to population declines (Dekker 2003; Knights & White 1998; Starkie 2003).

The European eel stock is considered outside safe biological limits and its fishery unsustainable (ICES 2007). In 2007, the European eel was listed under Appendix II of the Convention on International Trade in Endangered Species (CITES), and the European Union adopted Council Regulation 1100/2007/EC, requiring member states to prepare eel management plans (EMPs). Mitigating the impact of anthropogenic barriers on eel migration is highlighted in many EMPs as an important strategy for aiding stock recovery.

Fish passes are designed to aid upstream passage of fish at anthropogenic barriers (for an overview see Clay 1995). Common technical designs include: 1. pool type passes, which provide a series of stepped pools through which water flows downstream over weirs or through vertical slots, orifices or notches; or 2. steep compact passes (such as the Denil pass) which incorporate baffles to dissipate water energy as turbulence, thus reducing mean velocities to within the swimming capabilities of the target species (Clay 1995; Armstrong et al. 2004). While such designs may work, at least partially (see Noonan et al. 2012), for large bodied migrants with strong swimming and leaping capabilities (e.g. adult salmonids), they tend to be less effective in facilitating the upstream passage of smaller species (MacDonald & Davies 2007; Mallen-Cooper & Brand 2007) or those with elongated anguilliform body morphologies (e.g. eels, Feunteun 2002, and lampreys, Moser et al. 2002; Foulds & Lucas 2013). Juvenile eels have low burst swimming capabilities (e.g. in a swim chamber, 72 mm
elvers attained maximum burst speeds of ca. 50 cm s\(^{-1}\); McCleave 1980) and are unable to
reach or maintain the swimming speeds often required to ascend traditional fish passes, while
vertical differences in head between pools may pose a physical barrier as they cannot leap.
Fish pass design must therefore take their small size and poor burst swimming capability into
consideration. Conversely, their ability to climb wetted surfaces provides an opportunity for
novel species specific solutions. The high density of barriers to migration in the UK and
Europe (Kemp & O’Hanley 2010) necessitates that the fish pass design adopted must be cost
effective and simple to retrofit.
Eel specific bristle board passes have been developed and widely used for upstream
migrating juveniles, e.g. in the UK (Solomon & Beach 2004) and France (Porcher 2002).
Despite their apparent effectiveness in the field (Solomon & Beach 2004), there have been
few robust and controlled studies conducted to assess passage efficiency. Concerns have been
raised that bristles might clog with debris over time and may be less effective during high
flows. In the UK, as an alternative, ‘studded’ substrates have been developed recently as a
biologically and economically effective solution. There are precedents for the use of similar
designs. For example, a plastic studded substrate proved effective for inanga, Galaxias
maculatus (Jenyns), and redfin bullies, Gobiomorphus huttoni (Ogilby), ascending a 1.5 m
artificial ramp (Baker & Boubée 2006), and a ca. 9 m long studded eel ladder on the
Richelieu River (Canada) enabled American eel, Anguilla rostrata (Lesueur) to pass over a 5
m high weir (Verdon et al. 2003). In the UK, the studded boards, commonly referred to as eel
tiles, are frequently designed with a novel dual diameter stud dimension set at two different
densities (see ‘Materials and methods’ for detailed description) to facilitate a wide range of
body lengths. To date, the efficiency of eel tiles has not been independently evaluated, and an
understanding of swimming behaviour when attempting to ascend such passes is lacking.
The aim of this study was to assess effectiveness of eel tiles for facilitating upstream passage of juvenile European eels at an experimental Crump weir. Crump weirs, common barriers to fish migration in the UK (Lucas & Frear 1997; Lucas & Bubb 2005; Russon et al. 2010), are used to gauge river discharge as part of flood monitoring, and so retrofitting through installation of fish passes (Rhodes & Servais 2008) is preferred over their removal. This study used glass eels as they represent the earliest developmental stage expected to utilise eel passes, and have been observed congregating below anthropogenic barriers (Feunteun et al. 1998). Restricted upstream migration of this life-stage represents a bottleneck for recruitment, alleviation of which is considered a principal target for conservation efforts (Mouton et al. 2014). The first objective of this study was to quantify and compare upstream passage efficiency for an unmodified (no studded eel tiles on the downstream face; control) and modified (with eel tiles on the downstream face; treatment) model Crump weir. As eel tiles utilise a dual density stud design, the second objective was to determine whether stud configuration (dimension and spacing) influenced passage efficiency. The third objective was to quantify eel behaviour (in terms of activity and motivation, position reached on the weir face and swimming speed) when attempting to ascend the Crump weir.

Materials and methods

Experimental setup

Experiments were conducted in an indoor open channel flume (12.0 m long, 0.3 m wide, and 0.4 m deep) at the International Centre for Ecohydraulics Research, University of Southampton (UK). Discharge was constant (approximately 1 L s⁻¹) and plastic screens placed on the outside of the flume prevented visual disturbance to the test fish. A Crump weir (25 cm high) spanned the width of the experimental channel, with upstream and downstream
slopes of 1:2 and 1:5, respectively, in line with British Standards Institution (BS 3680-4B) criteria (Figure 1a). The ability of European glass eel to ascend the weir was tested under two setups: unmodified (control) and modified (treatment) with eel tiles placed on the downstream face. The tiles consisted of two ‘stud’ sizes (5 cm high; 3.0 and 1.5 cm max. diameter for the large and small stud, respectively), spaced 8.5 cm (large) or 4.5 cm (small) apart (measured from centre of the stud; Figure 1b).

Water velocities were measured (at 60% water depth) up- and down-stream of the weir using an electromagnetic flow meter (Valeport Model 801). A shallow (0.5 cm) sheet of water flowed over the downstream face of the weir, where velocity was measured only during the control treatment. Use of the flow meter was prevented when eel tiles were in place, so the time taken for 5 ml of India ink to flow down the weir face was recorded instead. Mean (± SD) water velocity upstream (control = 1.03 [± 0.64] cm s\(^{-1}\), modified = 0.80 [± 0.61] cm s\(^{-1}\)) and downstream (control = 7.11 [± 8.84] cm s\(^{-1}\), modified = 10.00 [± 9.52] cm s\(^{-1}\)) of the weir were similar between setups. During the control, water velocity accelerated as it flowed down the weir face, reaching a maximum of 73.7 cm s\(^{-1}\) (mean velocity: 57.4 [± 17.3] cm s\(^{-1}\)). During the treatment, average water velocity on the downstream weir face was estimated to be 34.7 cm s\(^{-1}\). Downstream water depth remained constant (5 cm) between setups, but upstream water depth was higher (27.8 versus 26.5 cm) when the tiles were in place.

**Fish maintenance**

Three hundred grams of glass eels (showing a small degree of pigmentation, but see Figure 1c), captured from the River Severn (UK) on the night of 2 May 2013, were transported in chilled (8°C) river water to the University of Southampton the following day, and placed in a 290 L holding tank under natural photoperiod. Holding tank water was chilled to 8°C and then allowed to increase by approximately 2°C per day until reaching ambient laboratory
temperatures before trials commenced. Mean holding tank water temperature at the beginning
of the experimental period was 18.8 (± 1.19) °C.

Experimental protocol

Ten 10 minute trials were conducted during daylight (10:00 to 17:00) for each of the two
setups between 7 and 9 May 2013. At the start of each day, up to 10 groups of 30 fish were
placed in perforated sealed tubes located at the upstream end of the flume and allowed to
acclimatise for a minimum of 1 hour before the start of the first trial. Flume water
temperature (mean ± SD = 21.8 ± 0.96 °C, comparable to some UK river temperatures during
late spring / summer e.g. the River Stour, East Anglia; Piper et al. 2012) was recorded before
30 fish were released 2.2 m downstream of the weir crest at the start of each trial. At the end
of each trial the fish were removed from the flume and weighed (mean mass ± SD = 0.35 ±
0.03 g), and measured (mean total length based on a sample of 10% of the test population ±
SD = 71.73 ± 3.87 mm). Each fish was used in one trial only.

Fish behaviour

Three overhead CCTV video cameras were used to record eel behaviour as they attempted to
ascend the weir, and analysis of the video footage allowed the following metrics to be
quantified:

Passage efficiency

During control trials, a passage attempt was deemed to occur when the head of an eel
progressed upstream of the hydraulic jump (15 cm up the weir face). As no hydraulic jump
was present during modified trials, a passage attempt occurred when the head progressed onto
the most downstream tile. A successful pass was recorded when the whole body of the fish
progressed over the weir crest. Passage efficiency was defined as the number of successful
passes expressed as a percentage of number of passage attempts, and compared between the
two setups (objective 1). Under the treatment condition the two stud types (small and large)
each covered 50% of the downstream weir face (Figure 1b). The number of eels that passed
the weir crest above the side of flume covered by small and large studs was recorded and
influence of stud configuration on passage efficiency assessed (objective 2).

Activity and motivation

Approaches (when an eel came within 5 cm of the downstream weir face) and attempts to
ascend the weir were used to indicate levels of activity and motivation, respectively, and
quantified as approach or attempt rate (mean number per minute per fish downstream of the
weir).

Position on weir face

The maximum distance of ascent (the most upstream point reached on the weir face during a
passage attempt, including those that succeeded) was quantified using video tracking
software (Logger Pro v3.8.2, Vernier Software, Beaverton, OR, USA). At the start of each
passage attempt, lateral position was categorised as being the true left (TL), true right (TR)
(i.e. the left or right side of the flume when looking downstream), or centre, assuming equal
channel division.

Swimming speed

A conservative estimate of swimming speed (i.e. assuming the shortest possible swim path)
was determined for each eel that successfully ascended the weir. Time to pass, between
initiating a passage attempt and the entire body passing over the weir crest was calculated.
Ground speed was calculated as the quotient of weir face length (1.25 m) and time to pass.
Swimming speed was estimated as the sum of mean water velocity and ground speed.

**Statistical analysis**

Data were tested for normality and homogeneity of variance using a Shapiro-Wilk and Levene's Test, respectively. When these assumptions were violated, data were log transformed. The number of fish that passed over the small versus large stud configuration and maximum distance of ascent was tested using an Independent samples $t$-test. Within each setup, differences between lateral position (TL, TR or Centre) were tested using one-way ANOVA with a Tukey post hoc test.

Owing to the non-linear relationship between approach (or attempt) rate and time, additive modelling was used to test whether there were differences between setups. Three candidate additive models were fitted which examined whether: 1. there was a relationship between approach (or attempt) rate and time, 2. the mean value of the relationship differed between setups, and 3. the shape of the relationship varied between setup. The models were fitted using a penalized regression spline from the 'mgcv' package in R (R version 3.03; R Core Team 2014; Wood 2003, 2004) which used cross-validation to determine the amount of smoothing (Zuur 2012). A thin plate regression spline was used for the smoother. The final model was determined as the candidate model with the lowest Akaike Information Criterion (AIC) value. For approach and attempt rate the assumptions of normality, homogeneity of variance, and independence were assessed by examining plots of the residuals against the fitted values and covariates. As the initial model fit violated the assumption of independence, the model was refitted using a Generalized Additive Mixed Model (GAMM) with an AR-1 auto-correlation structure. As the assumption of homogeneity was violated the GAMM was extended to incorporate a variety of variance structures (see Zuur et al. 2009). The structure
that produced the lowest AIC value was selected. A combined structure that allows for
different residual variation between the control and treatment, and power of the variance
covariate for time produced the best fit. For attempt rate, examination of the residuals
suggested a large outlier. Therefore, this trial was removed and the model re-run.

Results

Passage efficiency
Mean (± SD) number of passage attempts and passes were respectively 30.4 (± 13.0) and 0.0
(± 0.0) during the control. When eel tiles were installed, an average of 29.9 (± 6.1) and 20.0
(± 4.6) passage attempts and passes per trial were recorded, respectively (Figure 2), resulting
in a mean passage efficiency of 66.9% (objective 1). More eels passed the weir crest above
the small (11.7 ± 2.9) than large (8.3 ± 2.6) studs (t = 2.72, d.f. = 18, P < 0.05), with
corresponding mean passage efficiencies of 58.7% and 41.3% per trial, respectively
(objective 2).

Activity and motivation
The third candidate additive model had the lowest AIC value, indicating the shape of the
relationship between approach (and attempt) rate and time (minute) differed between setups
(Figure 3). There was no relationship between approach rate and time for the control \(F_{1.198} =
1.83, P = 0.177\), but a strong relationship for the treatment \(F_{6.14, 192.87} = 42.75, P < 0.001\).
Approach rate was initially higher for the treatment compared to the control (minutes 1, 2 and
3), but approximately equal between setups thereafter (Figure 3a). The final GAMM
explained 58.1 % of the variability in approach rate. A similar pattern was observed for
attempt rate (Figure 3b), with no relationship with time for the control \(F_{1.197} = 3.70, P =\)
0.056), but a strong relationship for the treatment \((F_{4,52,194.48} = 20.88, P < 0.001)\). The final
GAMM explained 39.1% of the variability in the number of passage attempts.

**Position on weir face**

Maximum distance of ascent was greater under the treatment \((t = -25.63, \text{ d.f.} = 18, P < 0.001)\), frequently culminating in successful passage (Figure 4). Under the control, the maximum distance of ascent was greatest at the channel edges (Figure 4a). Eels were generally edge oriented, with more passage attempts (control: \(F_{2.25} = 28.87, P < 0.001\);
treatment: \(F_{2.27} = 25.14, P < 0.001\)) along the channel sides (Table 1).

**Swimming speed**

Swimming speed was not calculated for the control as no eels successfully ascended the weir. Eels were not observed climbing or crawling through the eel tiles; instead they used anguilliform swimming to rapidly ascend the weir (mean ± SD time to pass the 1.25 m weir was 11.4 ± 3.53 sec, excluding 2 outliers where eels impinged on studs). Average swimming speed was estimated to be 50.02 cm s\(^{-1}\) during passage (range = 38.9 – 68.5 cm s\(^{-1}\)).

**Discussion**

This experimental study is the first to quantify fish passage efficiency for juvenile European eels utilising eel tiles to circumvent barriers to migration. The results support the findings of others; Crump weirs can pose a barrier to upstream migration, e.g. as for barbel, *Barbus barbus* L. (Lucas & Frear 1997), European grayling, *Thymallus thymallus* L. (Lucas & Bubb 2005), and river lamprey, *Lampetra fluviatilis* L. (Russon *et al*. 2010). Eel tiles facilitated upstream movement, improving passage efficiency from 0% to 67%.
The dual density of eel tile studs was intended to facilitate passage of a wide size range of eels. Under the conditions described in this study, eels tended to pass the weir crest above the side that contained small rather than large studs. For glass eels and similar sized elvers, the small stud design would likely be most effective at facilitating upstream passage at river infrastructure. In studies with similar synthetic substrates, stud (or bristle) density was often reported to be size selective, with high densities favouring smaller individuals (for an overview see Solomon & Beach, 2004). Accordingly, previous research has recommended adapting bristle/stud density according to the size distribution of eels expected to utilise the pass (Legault, 1992). The passage efficiency of the stud configurations tested in this study for larger eels requires further investigation. It appears that above a certain threshold body size, the smaller density studs become challenging for eels to navigate through (Vowles, unpublished).

Overall, glass eels were highly active and motivated to swim upstream, repeatedly approaching and attempting to ascend the weir under both setups. The high water temperatures observed during this study likely contributed to activity levels, with previous research demonstrating a positive relationship between water temperature and upstream movement for juvenile eel (White & Knights, 1988). Although at lower temperatures passage attempt rate will likely be lower, passage efficiency should not be compromised as long as water velocity remains within the swimming capability of the fish.

Although eels were motivated to progress upstream, for the first minute of the trials both approach and attempt rate were on average 4 fold greater during the treatment than the control. This difference in behaviour could be driven by hydrodynamic differences between setups. Eels may have been attracted to turbulence generated by water flowing around the staggered array of studs. Turbulence has been suggested as a potential attractant to eel passes (Solomon & Beach 2004), and in a field study elvers were twice as likely to use a bristle pass
with a more turbulent plunging, rather than streaming attraction flow (Piper et al. 2012).

Higher levels of turbulence may be expected under field scenarios, potentially enhancing
attraction and reducing delay for upstream migrating juvenile eels. However, benefits of
turbulence as a possible attractant should be considered in light of potential costs of impaired
passage performance, e.g. due to increased energetic costs of swimming (Enders et al. 2003)
and destabilisation (Tritico & Cotel 2010). Further, levels of attraction are likely to vary
between sites, due to volume of competing river discharge, or positioning of the pass. Indeed,
ensuring adequate attraction may well represent the largest challenge for juvenile eel passes,
which are typically designed to be narrow (30 – 45 cm) in width (Solomon & Beach, 2004).

Eel tile attraction and passage efficiency should be quantified and compared with suitable
alternatives through robust field studies.

Water accelerated as it flowed down the face of the unmodified weir, reaching
velocities in excess of the maximum burst swimming capabilities previously reported for
juvenile eels (e.g. 50 cm s⁻¹; McCleave 1980). Despite this, eels were able to progress 83 cm
up the weir face by taking advantage of lower velocities towards the channel sides. Indeed,
eels were edge oriented during both setups, an observation documented in other studies
(Tesch 2003; Piper et al. 2012). As a result, eel passes are typically situated at the edge of
barriers to maximise passage (Porcher 2002; Solomon & Beach 2004). In rivers, low-head
structures not traditionally considered to be major barriers to fish movement are likely to
impede upstream migrating juvenile eels unless velocities are sufficiently low, they have the
opportunity to climb suitable wetted margins (Linton et al. 2007), or eel specific passes are
provided (Solomon & Beach 2004).

Based on previous observations of behaviour at bristle passes, juvenile eels were
expected to ascend the tiles by climbing between the protruding studs. In this study, glass eels
used anguilliform swimming to ascend the weir, typically in one rapid burst. Relatively high
water temperatures likely increased swimming activity and ability (see Edeline et al. 2006),
leading to a greater propensity to burst swim against the flow. Alternatively, the gaps
between studs may have been too large and/or water velocities too great to enable climbing.
Eels that failed to pass in a single attempt were typically washed back downstream,
seemingly unable to maintain position on the face of the tile. When weir length and/or water
velocity is greater than the critical threshold for successful passage in a single burst of
activity, resting locations may be required to ensure tile performance is maintained.
The conservative estimate of swimming speed (50 cm s^{-1}) calculated during this study
closely matched the maximum burst capability of elvers (of an equivalent size) quantified
using a swim chamber (McCleave 1980). However, some glass eels attained speeds as high as
68.5 cm s^{-1}, indicating that they are able to reach higher swimming speeds than previously
reported when motivated to move upstream. Indeed, the swimming performance of other
species is greater than expected when the exhibition of volitional swimming is facilitated in
open channels, rather than when fish are forced to swim in confined chambers (Peake 2004;
Castro-Santos 2005; Russon & Kemp 2011). Nevertheless, swimming performance of glass
eels is low when viewed from a traditional fish passage perspective, where design velocities
are frequently around 250 – 300 cm s^{-1} (Clay 1995).

Conclusions

Given the conservation status and legislative protection afforded to European eels it is
important that potential barriers to their migration are assessed and impacts mitigated for. The
small size and low swimming performance of juvenile eels often renders traditional fish
passes ineffective for facilitating their upstream migration, necessitating development of
species specific passage solutions. This study quantified the efficiency of a dual density and
dimension ‘studded’ substrate (eel tiles) for glass eels. Passage efficiency over eel tiles was
67%, with the small stud spacing being more effective than the large. However, as successful
eels had to burst swim upstream in a single attempt, resting locations may be required for
larger barriers and / or when greater velocities are encountered. Further research is needed to
assess passage efficiencies under higher flows, for a wider size range of eel, and for other
migratory anguilliforms such as lampreys, for which traditional fishways are often ineffective
(Foulds & Lucas 2013). The performance of eel tiles should be validated through robust field
studies to advance the development of cost effective methods of alleviating habitat
fragmentation.

References

and Approval of Fish Passes in England and Wales. Environment Agency, Pembrokeshire,
Wales.

redfin bullies Gobiomorphus huttoni over artificial ramps. Journal of Fish Biology 69, 668-
681.

in glass eels entering the Gironde (France). Bulletin Français de la Pêche et de la
Pisciculture 378-379, 5-21.

volitional high-speed swimming behavior of migratory fishes. The Journal of Experimental
Biology 208, 421-432.
Chadwick S., Knights B., Thorley J.L. & Bark A. (2007) A long-term study of population characteristics and downstream migrations of the European eel *Anguilla anguilla* (L.) and the effects of a migration barrier in the Girkock Burn, north-east Scotland. *Journal of Fish Biology* 70, 1535-1553.


Acknowledgements

This study was funded by the Environment Agency, UK. We thank Peter Wood from UK Glass Eels for supply of fish, and Berry and Escott Engineering for providing the eel tile substrate.
Table 1. Lateral position of eels as they initiate an attempt to ascend an experimental Crump weir. Categories are true left (TL), true right (TR) or Centre, assuming equal channel division. Tukey Post hoc comparisons illustrate significant differences.

Figure 1. Dimensions of a model Crump weir used at the ICER experimental facility, University of Southampton (UK), to assess the ability of glass eels to pass upstream when unmodified (control) and modified with eel tiles on the downstream face (treatment) (a), a plan view of the eel tile stud sizes and configuration (b), and a sample of European glass eels (Anguilla anguilla L.) used during the trials to illustrate degree of pigmentation (c).

Figure 2. Mean (+1 SE) number of approaches (black bars), attempts (grey bars), and successful passes (clear bars) over a model Crump weir in 10 minutes.

Figure 3. The relationship between time and, (a) approach and (b) attempt rate. The shape of the relationship in both (a) and (b) varies between the control (dashed line, open circles) and treatment (solid line, filled triangles). N.B. the relationship between time and the control was not significant at $\alpha < 0.05$ (line added for interpretation).

Figure 4. Maximum distance and lateral position of glass eels that attempted to ascend an experimental Crump weir during (a) control (light grey dashed line indicates location of the hydraulic jump), and (b) treatment setups.
<table>
<thead>
<tr>
<th>Setup</th>
<th>Lateral position</th>
<th>Mean (± SD) number of attempts per trial</th>
<th>Post hoc comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>TR</td>
<td>11.8 (5.22)</td>
<td>TR vs. Centre: $P &lt; 0.001$</td>
</tr>
<tr>
<td></td>
<td>Centre</td>
<td>2.2 (1.81)</td>
<td>TR vs. TL: $P = 0.338$</td>
</tr>
<tr>
<td></td>
<td>TL</td>
<td>16.5 (9.63)</td>
<td>TL vs. Centre: $P &lt; 0.001$</td>
</tr>
<tr>
<td>Treatment</td>
<td>TR</td>
<td>14.1 (4.86)</td>
<td>TR vs. Centre: $P &lt; 0.001$</td>
</tr>
<tr>
<td></td>
<td>Centre</td>
<td>3.5 (1.65)</td>
<td>TR vs. TL: $P = 0.722$</td>
</tr>
<tr>
<td></td>
<td>TL</td>
<td>12.3 (3.47)</td>
<td>TL vs. Centre: $P &lt; 0.001$</td>
</tr>
</tbody>
</table>