Hydraulic synchrony of spawning sites amongst Earth's riverine fishes

Antóin M. O'Sullivan^{*1,2}, Alexander M. Morgan^{1,3,4}, Robert Newbury¹, Tommi Linnansaari^{1,2,3},
Barret L. Kurylyk⁵, Jani Helminen⁶, Bernhard Wegscheider⁷, Robert C. Johns⁸, Kurt Samways^{1,9},
Kari I. Alex¹⁰, R. Allen Curry^{1,2,3}, and Richard A. Cunjak^{1,2,3}

¹ Canadian Rivers Institute, University of New Brunswick (New Brunswick, Canada)

² FOREM, University of New Brunswick (New Brunswick, Canada)

³Biology, University of New Brunswick (New Brunswick, Canada)

⁴Physics, University of New Brunswick (New Brunswick, Canada)

⁵Civil and Resource Engineering, Dalhousie University (Nova Scotia, Canada)

⁶Fish and Water Research Ltd. (Klaukkala, Finland)

⁷Institute of Ecology and Evolution, Wyss Academy for Nature, University of Bern (Bern, Switzerland)

⁸Atlantic Forestry Centre, Canadian Forest Service, Natural Resources Canada (New Brunswick, Canada)

⁹Biology, University of New Brunswick (New Brunswick, Canada)

¹⁰Okanagan Nation Alliance Fisheries Department (British Columbia, Canada)

ORCIDs

- Antóin M. O'Sullivan - 0000-0003-0599-887X
- Tommi Linnansaari - 0000-0002-8594-3838
- Jani Helminen - [0000-0001-7358-8341](https://orcid.org/0000-0001-7358-8341)
- Rob C. Johns – 000-0002-8936-7735

*corresponding author: Antin M. O’Sullivan (aosulliv@unb.ca)

Abstract

Earth’s riverine fishes utilize a suite of reproductive guilds, broadly following four guilds: nest
guarders, broadcast pelagic spawners, broadcast benthic spawners and nest non-guarders ^{1, 2}, and
these guilds utilize different mechanisms to aerate eggs ^{3,4}. Globally, river fishes populations are
declining⁵, and spawning habitat rehabilitation has become a popular tool to counter these
declines⁶. However, there is a lack of understanding as to what classifies suitable spawning
habitats for riverine fishes, thereby limiting the efficacy of these efforts and thus the restoration
of the target species. Using data from $n = 220$ peer-reviewed papers and examining $n = 128$
unique species, we show the existence of a hydraulic pattern (defined by Froude number (Fr), a
non-dimensional hydraulic parameter) that characterizes the reproductive guilds of riverine
fishes. We found nest guarders, broadcast pelagic spawners, benthic spawners, and nest non-
guarders selected sites with mean $Fr = 0.05, 0.11, 0.22$, and 0.28 , respectively. Some of the
fishes in this study are living fossils, suggesting that that these hydraulic preference patterns may
be consistent across time. Our results suggest this hydraulic pattern can guide spawning habitat
rehabilitation for all riverine fish species globally in absence of specific spawning habitat
information for a species, where resource managers can establish the reproductive guild of the
species of interest, and then apply the specific hydraulic requirements (Fr range) of that
reproductive guild, as presented herein, in the rehabilitation of the target species.

Main

Throughout the year Earth's rivers pulse as their fishes spawn to complete their life cycle, thus ensuring the continued success of their respective species. Their selection of spawning sites is based on reproductive guilds, and these broadly (but not exclusively) follow four guilds^{1,2}: (i) nest builders that guard their nest (nest - guarder), *e.g.*, smallmouth bass (*Micropterus dolomieu*), (ii) nest builders that do not guard their nest (nest non-guarder), *e.g.*, Dwarf Ayu (*Plecoglossus altivelis*), (iii) broadcast pelagic spawners – fishes that spawn in the water column (broadcast - pelagic), *e.g.*, Darling River hardyhead (*Craterocephalus amniculus*) and (iv) broadcast benthic spawners – fishes that broadcast spawn onto substrates (broadcast - benthic)), *e.g.*, American paddlefish (*Polyodon spathula*). Regardless of the guild, a key to maturation and hatching of these eggs is adequate oxygenation^{3,4} – see Fig. 1. Nest builders, for instance, fan their nests to aerate their eggs, whereas nest non-guarders will create a nest that modulates river flow to aerate their eggs⁷.

Earth's riverine fishes are experiencing steep declines⁵. The reasons for this are multifaceted and linked to habitat degradation, dams, overharvest, introduction of non-native species, and climate change^{8,9}. With these declines, we are on the cusp of losing myriad species and the critical ecosystem functions and services they provide. To counter these declines, governmental and non-profit groups are turning to spawning habitat restoration^{6,10}. While this is a laudable aim, there is a lack of understanding as to what classifies suitable spawning habitats for riverine fishes, and it is infeasible to find this explicitly out for every riverine fish species. This knowledge gap serves to limit the efficacy of these efforts and thus the restoration of the target species. We hypothesize that a hydraulic pattern exists in the spawning habitats of Earth's riverine fishes, and this pattern can guide spawning habitat rehabilitation in absence of species-specific information. We select Froude number (*Fr*) as a non-dimensional hydraulic parameter that is comparable across all spatial scales, and has shown promise in previous studies examining detailed spawning characteristics (*e.g.*,^{10,11}). *Fr* is simply a ratio of inertial to gravity forces (see methods), and describes the river's hydraulic energy regime. We postulate, *a priori*, that low *Fr* values characterize the spawning habitats of nest guarders, where oxygenation of the eggs is provided by the parent. This energetically costly guild motivates the selection of a hydraulic regime that limits energetic expenditure associated with swimming (Fig. 1). Conceptually, as the reproductive guild changes, the hydraulic regime required to aerate the eggs is also predicted to

change. For instance, broadcast pelagic spawners that spawn semi-buoyant eggs are hypothesized to select different hydraulic regimes than broadcast benthic spawners that spawn adhesive eggs (Fig. 1). Contrastingly, we hypothesize that nest-non guarders select relatively higher Fr values to limit sedimentation accumulation in the nest that would reduce natural oxygenation (Fig. 1). To test our hypotheses, we conducted a meta-analysis of $n = 220$ peer-reviewed papers that describe depth and velocity conditions, and thereby Fr , at the spawning sites of $n = 128$ unique riverine fishes across the planet (Fig. 2a and Tables S1 and S2). These data include each of the four reproductive guilds detailed above (Fig. 1 and 2).

Fig. 1 The conceptual model illustrating our hypothesized relationship between global reproductive guilds and Froude number. A schematic of global riverine reproductive guilds (a), and their hypothesized relationship with oxygenation, and parental energetic investment in incubation (b) as a function of Froude number.

	Nest guarder	Broadcast pelagic	Broadcast benthic	Nest non-guarder	Total
No. of samples (<i>n</i>)	34	18	61	107	220
No. of species (<i>n</i>)	31	13	44	40	128

Fig. 2 Spatial extent of the data underlying our analysis displaying reproductive guild classification (color), sample size and number of unique species, and the total number of samples for each reproductive guild.

Results and Discussion

Globally, *Fr* values indicate an association with reproductive guilds that was not evident in depth or velocity (Fig. 3). Nest guarders, broadcast pelagic spawners, benthic spawners, and nest non-guarders selected sites with mean *Fr* numbers of 0.05, 0.11, 0.22, and 0.28, respectively (Fig. 3). We acknowledge that we observed between-population variability within species in the *Fr* at their spawning location. This means that the *Fr* at selected spawning sites is not necessarily a “crisp” number and some inherent variability is assumed. However, we tested the validity of the observed patterns in *Fr* by examining species specific *Fr* estimates (*i.e.*, for multiple single species observations, we reduced the parameter of interest to the mean of the total observations), and the results remain the same (see methods and Fig. 3a-c and d-f). As such, our meta-analysis supports the hypothesis, and conceptual model, that a hydraulic pattern, as represented by *Fr*, is apparent from the reproductive guilds of Earth’s riverine fishes (Figs. 1 and 3.).

Fig. 3 Descriptive statistics results illustrating the relationship between depth, velocity and Froude number values for nest guarders, broadcast pelagic, broadcast benthic, and nest non-guarding reproductive guilds stratified as per our conceptual model (Fig. 1) for the entire data set ($n = 220$) (a-c), and unique species ($n = 128$) (d-f).

Nest guarders selected sites with the lowest Fr values observed across the $n = 128$ species examined. Nest guarders, such as the eel tailed catfish (*Tandanus tandanus*), are uniquely characterized in our dataset by a parent that protects and aerates the nest. It is well established that providing parental care is energetically costly, with links to reduced parental growth¹². Biotic interactions by predators can further exacerbate energetic costs for nest guarders (e.g., smallmouth bass (*Micropterus dolomieu*) and round goby (*Neogobius melanostomus*) – see¹³). We investigated the role of Fr on energetic expenditure for nest guarders using an integrated Froude number – Strouhal number model ($Fr-St$), where St is a dimensionless number that describes oscillating flow mechanisms. Considering nest guarders fan their nest to remove fine sediments and aerate their eggs, we assume $St = 0.3$ as this provides the greatest propulsion to entrain particles and aerate eggs (e.g.,^{14,15}). Examining the relationship between Fr and tail-beat

frequency (f) reveals the energetic expenditure required to obtain optimal St – see methods. The Fr - St model suggests Fr values selected by nest guarders are energetically more efficient than the other reproductive guilds (see f values in Table 1). We thus propose the global occurrence of low Fr values for nest guarders is linked to energetic conservation of the parent, facilitating removal of fine sediments and aerating eggs in the most energetically efficient manner.

Table 1 Integrated Froude number (Fr) and Strouhal number (St) model results for different Fr scenarios associated with each reproductive guild quantifying how an increase in Fr while retaining an optimal $St = 0.3$ ¹⁵, leads to an increase in tail beat frequency f (see SI for full model).

	Reproductive guild			
	<i>Nest guarder</i>	<i>Broadcast pelagic</i>	<i>Broadcast benthic</i>	<i>Nest non- guarder</i>
Fr	0.08	0.11	0.22	0.28
St	0.3	0.3	0.3	0.3
$f (s^{-1})$	1.6	2.2	4.3	5.5

The role of hydraulics for the remaining three reproductive guilds is markedly different from nest guarders. When broadcast pelagic spawners spawn in the water column, their eggs can either settle onto vegetation or drift, *e.g.*, common bream (*Abramis brama*) and black carp (*Mylopharyngodon piceus*), respectively. For species whose eggs are deposited on vegetation, Fr values of ~ 0.11 likely produce an environment that aerates the eggs, while the presence of the vegetation limits shear stress and egg entrainment¹⁶. For species that spawn directly into the water column, we hypothesize a different link between the egg and the hydraulics. Here, we use striped bass (*Morone saxatilis*) as an example. Upon fertilization, the semi-buoyant striped bass eggs drift in the water column, with eggs becoming denser as they grow^{17,18}. In still water, ergo with little drag force, these denser eggs will sink, reducing survival¹⁹. As such, we suggest the selection of $Fr \sim 0.11$ for this guild provides adequate flow to entrain the eggs, and as the egg density increases, this hydraulic condition facilitates the egg staying buoyant, *i.e.*, prevent complete sinking, and allows time for the egg to hatch (Fig. 1).

The hydraulic controls on nest building non-guarders' site selection have been well studied^{20,21}. Salmonid redds, for instance, are understood to induce hyporheic flow paths (blue arrows Fig. 1) that remove fine sediments and metabolic by-products, while also aerating eggs, and creating a stable thermal environment²². These same mechanisms most likely transcend to other nest building non-guarders, such as sea lamprey (*Petromyzon marinus*) – see Table S1. However, less is understood about the role of hydraulics for broadcast benthic spawners, such as the robust redhorse (*Moxostoma robustum*) and alligator gar (*Atractosteus spatula*). Given both nest non-guarders and broadcast benthic spawners select gravel and cobble substrata, and the *Fr* values for both are the highest across the reproductive guilds, we postulate a similar hydraulic mechanism in both instances. Nonetheless, the difference in *Fr* for each guild does suggest subtle mechanistic differences. Broadcast benthic spawners eggs are typically adhesive¹. The eggs of Asp (*Leuciscus aspius*), for instance, are both negatively buoyant and adhesive²³. It is also well documented that benthic spawner eggs drop into interstitial voids^{6,24}. For broadcast benthic spawners (that spawn on complex bedforms with high hydraulic conductivity (*K*) substrate), we hypothesize the following: (a) *Fr* values ~ 0.22 induce hyporheic flows in the uppermost section of the substrate²⁵; and (b) the adhesive nature of the eggs offsets shear stress and uplift from the bulk flow and hyporheic flow, respectively, thus defining a different guild to exploit the hydraulics in comparison to nest non-guarders (Fig. 1). Similarly, nest non-guarders typically select spawning habitats that are also characterized by complex bedforms with high *K* sediments, and these induce hyporheic flow²⁶. However, nest building non-guarders are suggested to select sites with higher *Fr* values (Fig. 3). Nest building non-guarders do not typically have adhesive eggs and will bury their eggs post fertilization in a redd *e.g.*, brook trout (*Salvelinus fontinalis*) and barbel (*Barbus barbus*). We hypothesize the following for the suggested higher *Fr* values (a) higher *Fr* values will entrain fine sediments during nest construction, and this winnowing is understood to change *K* and thereby down and upwelling flux²², and (b) as the eggs of nest building non-guarders are buried, higher *Fr* values are likely required to increase oxygen in the nest²⁷.

Some of the fishes in this study can be considered living fossils. The lamprey (*Petromyzontiformes*) and the American paddlefish (*Polyodon spathula*) have existed since the Early Cretaceous^{28,29}, as such we hypothesize that that these hydraulic preference patterns with

reproductive guilds may be consistent across time. This simple Fr model foregoes consideration of many other important factors, including temperature and nutrients^{30,31}. For instance, groundwater upwelling may provide both aeration and thermal stability for eggs, thus limiting the requirement to select specific hydraulics, *e.g.*,³². However, the simple Fr model presented herein for four reproductive guilds does provide compelling evidence that the hydraulics that underpin the spawning habitats of the Earth's fishes are best characterized by Fr . The success of utilizing Fr values to rehabilitating spawning habitat is already evident in some rivers. Sockeye salmon (*Oncorhynchus nerka*), for instance, have been observed to select spawning habitats with $Fr = 0.32 (\pm 0.1)$ ¹⁰. Sockeye spawning habitat in the Okanagan River (British Columbia, Canada) was severely degraded in the 1950's when > 90 % of the river was straightened and dyked³³. Between 2014 - 2018, the channelized river was modified with spawning platforms designed to meet $0.2 \leq Fr \leq 0.4$ during the spawning autumn period³⁴. These spawning platforms have been utilized by sockeye salmon each year post-construction and have become a critical tool in rehabilitating sockeye salmon. The main finding of the work presented herein is that while it is unfeasible to describe in detail the spawning habitat requirements for all approximately 15 000 freshwater fish species³⁵, it may be sufficient to first establish the reproductive guild of the species of interest, and then apply suitable target Fr range, as presented herein, in rehabilitation to meet specific hydraulic requirements of the target species. Future conservation and/or restoration projects that target spawning habitat would therefore benefit from utilizing the link between reproductive guild and Fr range.

Methods

Meta-analysis data search

We conducted searches in multiple article databases using several different search terms to acquire as many peer-reviewed papers as possible. The search terms and database developed for this study are available in the supplementary information as an .xlsx file.

Froude number model

Froude number (Fr) is a non-dimensional hydrodynamic parameter that is calculated by:

$$Fr = \frac{V}{\sqrt{gD}} \quad (1)$$

where V is water velocity ($\text{m}\cdot\text{s}^{-1}$), g is the gravitational constant = $9.81 \text{ m}\cdot\text{s}^{-2}$ and D is depth (m).

221

222 ***Integrated Froude number – Strouhal number model***

223 A Strouhal number (St) is a non-dimensional hydrodynamic parameter that describes oscillating
224 flow mechanisms or vortex shedding in a fluid. Myriad experiments have shown that optimal St
225 values for swimming animals, defined by maximum propulsive efficiency, range from 0.25 to
226 0.35 (Taylor *et al.*, 2003). For fishes, St can be calculated by (Eloy, 2011):

$$227 \quad St = \frac{fA}{V} \quad (2)$$

228 where f is the tail-beat frequency (s^{-1}), A is the peak-to-peak tail amplitude (m), and V is water
229 velocity ($m \cdot s^{-1}$).

230 The f term can be isolated by rearranging equations (1) and (2), yielding the following form for
231 the integrated Froude number – Strouhal number mode ($Fr-St$) :

$$232 \quad f = \frac{Fr \cdot St \cdot \sqrt{gD}}{A} \quad (3)$$

233 ***Descriptive statistics***

234 We used univariate box plots to examine the relationship each hydraulic parameter and our
235 reproductive guild conceptual model. To account for instances when we had multiple within-
236 species observations, we reduced the observations to one per species to retain equal weights for
237 each species. In such instances, the average of the hydraulic parameters associated with that
238 species were calculated and used for the unique species analysis.

239 ***Acknowledgements***

240 First, the authors would like to thank Lord Pisces. We also thank the Atlantic Salmon
241 Conservation Foundation and New Brunswick Innovation Foundation for funding support.
242 AMM was funded by New Brunswick's Wildlife Trust Fund. We would also like to thank those
243 scientists whom conducted the studies that underpinned this research.

244 ***Funding***

245 Atlantic Salmon Conservation Foundation; New Brunswick Innovation Foundation; New
246 Brunswick's Wildlife Trust Fund.

247 ***Author contributions***

248 Conceptualization: AMO'S; RA Cunjak; Methodology: AMO'S; JH; BW; TL; Investigation:
249 AMO'S; AMM; Visualization: AMO'S; RJ; Funding acquisition: AMO'S, RA Curry, TL;

Project administration: AMO'S; Supervision: AMO'S; Writing – original draft: AMO'S; Writing
– review & editing: AMO'S; AMM, RN, RJ, TL, BLK, BW, JH, KL, RA Curry, KMS, RN, RA
Cunjak

Competing interests

The authors declare no competing interests.

Materials & Correspondence

Requests can be sent to Antóin M. O'Sullivan (aosulliv@unb.ca).

Data availability

The supporting data is available as supplementary information.

References

1. Keenleyside, M. H. A. *Diversity and Adaptation in Fish Behaviour*. **11**, (Springer Berlin Heidelberg, 1979).
2. Helfman, G. S., Collete, B. B., Facey, D. E. & Bowen, B. W. *The diversity of fishes*: biology, evolution, and ecology. (Wiley-Blackwell, 2009).
3. Kinne, O. & Kinne, E. M. Rates of Development in embryos of a cyprinodont fish exposed to different temperature-salinity-oxygen combinations. <https://doi.org/10.1139/z62-025> **40**, 231–253 (1962).
4. Rombough, P. J. Oxygen as a constraining factor in egg size evolution in salmonids. <https://doi.org/10.1139/f07-047> **64**, 692–699 (2007).
5. Su, G. *et al.* Human impacts on global freshwater fish biodiversity. *Science* (80-.). **371**, 835–838 (2021).
6. Manny, B. A. *et al.* A scientific basis for restoring fish spawning habitat in the St. Clair and Detroit Rivers of the Laurentian Great Lakes. *Restor. Ecol.* **23**, 149–156 (2015).
7. Cooke, S. J. & Schreer, J. F. Determination of fish community composition in the untempered regions of a thermal effluent canal-the efficacy of a fixed underwater videography system. *Environ. Monit. Assess.* **73**, 109–129 (2002).
8. Clausen, R. & York, R. Global biodiversity decline of marine and freshwater fish: A cross-national analysis of economic, demographic, and ecological influences. *Soc. Sci. Res.* **37**, 1310–1320 (2008).
9. Vörösmarty, C. J. *et al.* Global threats to human water security and river biodiversity. *Nat.* **467**, 555–561 (2010).
10. Long, K. I. The effects of redd site selection and redd geometry on the survival of incubating Okanagan sockeye eggs. (University of New Brunswick, 2007).
11. Moir, H. ., Soulsby, C. & Youngson, A. . Hydraulic and sedimentary controls on the availability and use of Atlantic salmon (*Salmo salar*) spawning habitat in the River Dee

- 285 system, north-east Scotland. *Geomorphology* **45**, 291–308 (2002).
- 286 12. Sargent, R. C. Paternal care and egg survival both increase with clutch size in the fathead
287 minnow, *Pimephales promelas*. *Behav. Ecol. Sociobiol.* 1988 231 **23**, 33–37 (1988).
- 288 13. Steinhart, G. B., Marschall, E. A. & Stein, R. A. Round Goby Predation on Smallmouth
289 Bass Offspring in Nests during Simulated Catch-and-Release Angling. *Chang. Publ.*
290 *Wiley* **133**, 121–131 (2011).
- 291 14. Taylor, G. K., Nudds, R. L. & Thomas, A. L. R. Flying and swimming animals cruise at a
292 Strouhal number tuned for high power efficiency. *Nat.* 2003 4256959 **425**, 707–711
293 (2003).
- 294 15. Eloy, C. Optimal Strouhal number for swimming animals. *J. Fluids Struct.* **30**, 205–218
295 (2012).
- 296 16. Termini, D. Experimental analysis of the effect of vegetation on flow and bed shear stress
297 distribution in high-curvature bends. *Geomorphology* **274**, 1–10 (2016).
- 298 17. Jr., N. M. H. *Transport simulation of striped bass eggs in the Congaree, Wateree, and*
299 *Santee rivers, South Carolina. Water-Resources Investigations Report* (1991).
300 doi:10.3133/WRI914088
- 301 18. Andrews, S. N., Dadswell, M. J., Buhariwalla, C. F., Linnansaari, T. & Curry, R. A.
302 Looking for Striped Bass in Atlantic Canada: The Reconciliation of Local, Scientific, and
303 Historical Knowledge. *Northeast. Nat.* **26**, 1 (2019).
- 304 19. Faber, D. J. & McAllister, D. E. Development of Fishes of the Mid-Atlantic Bight. An
305 Atlas of egg, larval and juvenile stages. <https://doi.org/10.1139/f79-107> **36**, 706–707
306 (2011).
- 307 20. Moir, H. J., Soulsby, C. & Youngson, A. Hydraulic and sedimentary characteristics of
308 habitat utilized by Atlantic salmon for spawning in the Girnock Burn, Scotland. *Fish.*
309 *Manag. Ecol.* **5**, 241–254 (1998).
- 310 21. Goode, J. R. *et al.* Potential effects of climate change on streambed scour and risks to
311 salmonid survival in snow-dominated mountain basins. *Hydrol. Process.* **27**, 750–765
312 (2013).
- 313 22. Tonina, D. T. & Buffington, J. M. B. M. A three-dimensional model for analyzing the
314 effects of salmon redds on hyporheic exchange and egg pocket habitat.
315 <https://doi.org/10.1139/F09-146> **66**, 2157–2173 (2009).
- 316 23. Mills, C. A. The attachment of dace, *Leuciscus leuciscus* L., eggs to the spawning
317 substratum and the influence of changes in water current on their survival. *J. Fish Biol.*
318 **19**, 129–134 (1981).
- 319 24. Roseman, E. F. *et al.* Lake sturgeon response to a spawning reef constructed in the Detroit
320 river. *J. Appl. Ichthyol.* **27**, 66–76 (2011).
- 321 25. Tonina, D. & Buffington, J. M. Hyporheic exchange in gravel bed rivers with pool-riffle
322 morphology: Laboratory experiments and three-dimensional modeling. *Water Resour.*

Res. **43**, 1421 (2007).

26. Magliozzi, C., Grabowski, R. C., Packman, A. I. & Krause, S. Toward a conceptual framework of hyporheic exchange across spatial scales. *Hydrol. Earth Syst. Sci.* **22**, 6163–6185 (2018).
27. Buffington, J. M. & Tonina, D. Hyporheic Exchange in Mountain Rivers II: Effects of Channel Morphology on Mechanics, Scales, and Rates of Exchange. *Geogr. Compass* **3**, 1038–1062 (2009).
28. Near, T. J. *et al.* Resolution of ray-finned fish phylogeny and timing of diversification. *Proc. Natl. Acad. Sci.* **109**, 13698–13703 (2012).
29. Chang, M., Wu, F., Miao, D. & Zhang, J. Discovery of fossil lamprey larva from the Lower Cretaceous reveals its three-phased life cycle. *Proc. Natl. Acad. Sci.* **111**, 15486–15490 (2014).
30. Sandströ, O., Abrahamsson, I., Andersson, J. & Vetemaa, M. Temperature effects on spawning and egg development in Eurasian perch. *J. Fish Biol.* **51**, 1015–1024 (1997).
31. Malzhan, A. M., Aberle, N., Clemmesen, C. & Boersma, M. Nutrient limitation of primary producers affects planktivorous fish condition — Sultan Qaboos University House of Expertise. *Mar. Sci. Fish.* **52**, 2062–2071 (2007).
32. Curry, R. A. & Noakes, D. L. G. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* **52**, 1733–1740 (1995).
33. Newbury, R. *Stream Restoration Hydraulics: Project Casebook*. (Newbury Hydraulics, 2016).
34. Rivard-Sirois, C., Alex, K. & Squakin, J. *Aquatic Monitoring 2017 Penticton Channel Salmon Spawning Restoration Work*. (2018).
35. Tedesco, P. A. *et al.* A global database on freshwater fish species occurrence in drainage basins. *Sci. Data* **2017 41** **4**, 1–6 (2017).