# Evaluating Egg Mats as a Method for Identifying White Sturgeon Spawning Habitat Characteristics

**by**

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# Abstract

Recovering species at risk requires careful consideration of their biology to identify the environmental needs that underpin restoration efforts. Endangered Nechako white sturgeon's recovery is faltering due to ongoing recruitment failure in early life stages, thus developing our understanding can help define the underlying mechanisms behind it. This study sought to evaluate egg mats as a way of identifying white sturgeon spawning habitat characteristics through use of experimentation and modeling techniques. The experiment revealed how the number of embryos on an egg mat relates to where sturgeon spawned. These parameters informed generalized additive models fit to simulated egg mat data, which determined whether spawning site characteristics can be identified using historic egg mat data. This study outlines the deposition rate of embryos on egg mats, and demonstrates that egg mat data alone is not enough to establish what environmental variables influence fine-scale sturgeon spawning site selection.

**Keywords**:    Nechako; Sturgeon; Egg Mat; Spawning Probability; River; Habitat Association

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# List of Acronyms

AIC                      Akaike Information Criterion

CSTC                 Carrier Sekani Tribal Council

GAM                    Generalized Additive Model

GLM                    Generalized Linear Model

NWSCC           Nechako White Sturgeon Conservation Centre

SFU                     Simon Fraser University

# Chapter 1.

# Background

Sturgeon are a fish belonging to the order Acipenciformes, and are the most threatened order of vertebrae in the world (IUCN, 2022). Despite substantial recovery efforts, white sturgeon (*Acipenser transmontanus*) have been documented to be declining throughout their ranges (Crossman & Hildebrand, 2022). Population declines in North America have been linked to multiple stressors including, but not limited to: loss of habitat quality and quantity, habitat fragmentation, altered hydrograph components, pollution, and fishing effort, (Fisheries & Oceans Canada, 2014). For some population groups of white sturgeon in British Columbia, naturally-spawned juvenile sturgeon are not suspected to survive to maturity in the quantities necessary to support future populations, as they are experiencing chronic recruitment failure (Fisheries & Oceans Canada, 2014).

The way white sturgeon have been categorized in British Columbia has changed over time. In the 2003 COSEWIC report, white sturgeon were classified into six "Nationally Significant Populations" (NSPs), as this is how white sturgeon are categorized under the Species at Risk Act (SARA). Since then, the species has been reassessed and categorized according to discrete and evolutionarily significant "Designatable Units" (COSEWIC, 2012; COSEWIC, 2012a). Currently, four DUs of white sturgeon exist in British Columbia: the Lower Fraser (Fraser River estuary to Hells Gate), the Upper Fraser (Hells Gate to the confluence of Morkill River and Fraser River), the Upper Columbia (Washington border to Kinbasket Lake in Canada) and the Upper Kootenay (Canadian portion of Kootenay watershed upstream of Corra Linn Dam, including Duncan Lake; COSEWIC, 2012). The Nechako white sturgeon is one of the three groups of white sturgeon that make up the Upper Fraser DU (COSEWIC, 2012). Nechako white sturgeon have been listed as an endangered NSP since 2006 under SARA (Fisheries & Oceans Canada, 2014), which prohibits the fishing, harvesting, or killing of the individuals.

The listing of Nechako white sturgeon as endangered followed the low population estimates and recognition of recruitment failure for the species. Recruitment failure for

Nechako white sturgeon was first identified as a problem for the species after a study estimated the population size of Nechako white sturgeon to be 571 fish (RL&L Environmental Services, Ltd. 2000). It was later estimated in 2006 that only about 305 mature fish existed in the population, and that the number was projected to decline to 25 by the year 2025 without intervention (Korman and Walters, 2001; Wood et al., 2007). Since its discovery, recruitment reconstruction for the Nechako white sturgeon population reveals that the rapid decline in recruitment began in 1967, and has remained very low in the years following (McAdam et al., 2005). Evaluation and potential causes of recruitment failure were presented by Korman and Walters (2001), and since then, efforts have continued to uncover the cause and mechanism of recruitment failure (McAdam et al., 2005; McAdam, 2012; Gauthier-Fauteux et al., 2022).

Recruitment failure for Nechako white sturgeon is hypothesized to be caused by larval sturgeon habitat loss through the process of "interstitial infilling". Interstitial infilling is a process that occurs when fine sediments settle and fill the small gaps (known as interstitial spaces) between substrates. Interstitial spaces are important for early sturgeon survival, particularly for yolksac larvae, as hiding in these spaces in the first days post-hatch have been found to increase their survival by sheltering them from predators and fast waters that would force them to drift downstream from spawning grounds (Gross et al., 2002; McAdam, 2012).

The life history of Nechako white sturgeon adds a layer of complexity to their management and conservation. Given individuals first reach maturity at 26 to 30 years of age and have a maximum lifespan exceeding 100 years (COSEWIC, 2012), sturgeon must survive many years before having an opportunity to reproduce. Although it takes a long time for white sturgeon to reach maturity, they are known to be highly fecund broadcast spawners. In Canada, medium sized female white sturgeon have fecundity ranging from 700,000 to four million eggs (Scott and Crossman, 1973). While a single female is capable of spawning many eggs, females only spawn once every three to five years, whereas males tend to spawn more frequently (Haxton et al., 2016).

Sturgeon spawning sites are determined by multiple environmental variables. For example, Lake Sturgeon (*A. fulvescens*) have been found to spawn at select locations where artificial reefs are present (Fischer et al., 2018). Specific velocities have been found to be of importance for white sturgeon (Paragamian et al., 2009; Parsley et al.,

1993), and it has been found that green sturgeon (*A. medirostris*), Atlantic sturgeon (*A. oxyrinchus*), and white sturgeon aggregate in deep areas of water to spawn (Hatin et al., 2002; Paragamian et al., 2009; Wyman et al., 2018). Interactions between these variables of location, substrate, velocity and depth have also been suggested to influence spawning site selection. On a finer scale, it has been suggested that some sturgeon will seek out the highest velocities and deepest depths within a spawning reach as the area in which they choose to spawn (McDonald et al., 2010; Paragamian et al., 2002).

Nechako white sturgeon are only known to spawn in one place, located within the district of Vanderhoof, BC. The spawning grounds exist between river kilometers (RKM) 135.6 and 139 of the Nechako River (with RKM 0 being the Nechako-Fraser confluence in Prince George, and RKM 291.5 being Kenney Dam). Spawning occurs within this 3.4 km spawning reach between May and July every year. Flows in the Nechako River at this spawning reach have been regulated by the upstream Kenney Dam, since its construction in 1952. These regulated flow patterns, and their influence on riverine habitats, has resulted in a divergence from historic conditions for the Nechako, as mean annual discharge is now reduced to approximately half of its pre-regulated condition in the Vanderhoof spawning area (NHC, 2003). These changes have resulted in complications in the conservation of Nechako white sturgeon.

Current conditions in the river make reversal of interstitial infilling challenging. In conjunction with alterations to the natural Nechako hydraulic system as a result of the Kenney Dam, sediment is continually being deposited in the Nechako in response to other growing anthropogenic industries such as forestry and agriculture (Gateuille et al., 2019; Hartman, 1996), as well as natural bank erosion. Given reduced flows of the Nechako River since construction of the Dam, infilled substrates are not expected to be reversed naturally given the scour velocities of the regulated river are not as strong as they were historically (NHC, 2003). Furthermore, increasing river flows to that of their natural conditions as a solution is not possible given the extent of municipal development that has been built in the historic floodplain (Mesa Muñoz & Trimiño Barbosa, 2015).

Multiple efforts to overcome these challenges and support recovery of the population are ongoing. The Nechako White Sturgeon Conservation Centre (NWSCC) has been

releasing hatchery-origin juvenile Nechako white sturgeon into the river since 2015. This hatchery captures wild adults in the river, breeds them, and raises their offspring to one or two-year old juveniles, in an effort to get individuals past their primary juvenile survival bottlenecks. Despite these efforts to supplement the population, mortality rates in hatchery-released juveniles are higher than anticipated, with an approximate 50% survival rate 12 months post-release, and as low as a 33% survival rate 24 months post-release (Nechako White Sturgeon Recovery Initiative, 2021). In addition to the hatchery program, the NWSCC and the Carrier Sekani Tribal Council (CSTC) work in tandem to monitor adult and juvenile movement through telemetry programs, and use egg mat monitoring as a means of collecting naturally-spawned embryos, determine spawning reach extent, and determine spawn timing.

The use of egg mats to monitor spawn timing, detect spawning-reach range, and, in recent years, collect naturally-spawned embryos, has been conducted annually since 2004. Egg mats are large metal-framed square structures with mats made of fibrous material, and are deployed throughout the spawning reach in various spatial configurations. Egg mats sit at the bottom of the river and act as a substrate on which adhesive negatively-buoyant embryos attach (McCabe & Beckman, 1990). Egg mats in the Nechako River are usually recovered after two days. Captured embryos counts are recorded for each egg mat before they are collected and delivered to the NWSCC for incubation. There are many ways of arraying egg mats, with some common strategies being: setting out egg mats in random locations (e.g., Rust et al., 2007): setting egg mats up in a grid array (e.g., Duncan et al., 2004; Thiem et al., 2013); placing egg mats at specific location-based sites (e.g. Roseman et al., 2020); or placing egg mats along a transect (e.g., Gillespie et al., 2020). Not only does the array change, but the number of egg mats deployed at a site can too, as egg mats can be either placed down as individual mats, or in groups of two or more at the same site (e.g., Nichols et al., 2003; Paragamian et al., 2001; Roseman et al., 2011). Historically, the way egg mats have been arrayed in the Nechako has changed from year-to-year, and sometimes, within a sampling season.

Recovery efforts involving habitat restoration and wild-spawned embryo collection could be enhanced if researchers can identify, or predict, spawning sites of white sturgeon. Habitat restoration could be targeted to fine-scale areas identified as conducive to sturgeon spawning and resulting embryo depositions. Examples of techniques that have

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been performed historically include: depositing clean gravel (NHC, 2012), and cleaning existing gravel of fine sediments (NHC, 2016; NHC, 2021). These remediation efforts are anticipated to improve larval survival and subsequently contribute to the recruitment of naturally-spawned, genetically-diverse wild juveniles. Despite the promise habitat restoration and remediations projects hold, it has been cautioned that they may not be efficient long-term if substrate infilling continues to affect restored areas (McAdam et al., 2018). Aside from, and in addition to habitat restoration efforts, the use of informed egg mat placement in locations likely to capture increased numbers of wild-spawned embryos could be strategized. These embryos could then be raised in the hatchery, similarly improving survival of genetically-diverse wild-spawned offspring.

Several methods are used by researchers working across sturgeon species to identify spawning locations and habitat use. These strategies include, but are not limited to: hydroacoustic devices such as dual-frequency identification sonars (DIDSON) and side-scan sonars (SSS) (Auer and Baker, 2007; Crossman et al., 2011; Golder Associates Ltd, 2009; Vine et al., 2019), acoustic telemetry tagging strategies (Colborne et al., 2019; Pendleton et al., 2019), egg mats (Chiotti et al., 2008), or some combination of these strategies (Caswell et al., 2004; Izzo et al., 2022). Given that egg mat data has been recorded historically for Nechako white sturgeon, researchers hope to opportunistically utilize it to identify sturgeon spawning locations. Considering measurements of environmental variables such as velocity, depth and location were occasionally sampled at the time of deployment and or recovery of egg mats, it has been the hope of researchers that these historic data may potentially provide insight to the environmental variables influencing sturgeon spawning site selection.

This thesis aims to evaluate egg mats as an approach for determining habitat characteristic associations with white sturgeon spawning site selection. To address uncertainties around how many embryos are likely to be caught by egg mats downstream from spawning locations, a field experiment was conducted to measure depletion rates of free-floating embryos with distance downstream. Findings from the field experiment were used to simulate spawning and embryo dispersal through the river, and their eventual capture by egg mats, which were simulated in different spatial configurations within the spawning reach. These simulated captures are analysed using a Generalized Additive Model (GAM) to evaluate, firstly, how predicted spawning probabilities based on these data compares to actual spawning probabilities, and,

secondly, to determine if the ques Nechako white sturgeon use when deciding spawning locations can be successfully determined using model selection. Ultimately, this thesis aims to answer two key questions: (1) what does the number of embryos on an egg mat tell researchers about where a sturgeon spawned? And (2) can egg mat data be used to determine what environmental variables Nechako white sturgeon use to select spawning sites?

# Chapter 2.

# Evaluating Egg Mats as a Method for Identifying White Sturgeon Spawning Habitat Characteristics

## 2.1. Introduction

The recovery of species at risk is a costly task (Schultz et al., 2013) that requires deliberate strategy and careful consideration of species' biology (Schneider, 2023; Wilcove & Chen, 1998). One of the key considerations for recovering a species at risk is determining what threatens their survival in the first place (McCune et al., 2013). In some instances, threats have been found to target specific life stages of the species, whether that be early (such as rising temperatures affecting thermally sensitive fish embryo development; Brett, 1952; Jatteau et al., 2017), mid (such as loggerhead sea turtle (*Caretta caretta*) juvenile survival being threatened by surface longlines and trawling fisheries; López-Mendilaharsu et al., 2020), or late (such as spawning fish being sensitive to the thermal responses as a result of climate change; Dahlke et al., 2020). In the case of fish species where early life stages are threatened, identifying locations and habitats associated with adult spawning and juvenile rearing allows focused restoration to bolster conditions that improve the survival of those stages. For example, it has been found that supplementing spawning grounds of some fish species with improved substrates can increase the abundance of fish that spawn there (Taylor et al., 2019). However, this requires an understanding of habitat usage at these life stages, which is notoriously difficult to gather when populations are at low abundance (Walsh et al., 2018).

Rivers are dynamic habitats that affect spawning behaviours of many fish species. Given the seasonal variability of river conditions, fish species that reside in rivers have developed life histories to help them adapt to these conditions (e.g., Tedesco et al., 2008; Winemiller 1989; Winemiller & Rose, 1992). Fish eggs spawned in riverine systems may distribute into downstream habitats as a result of high water-flows (e.g., Durham & Wilde, 2009), which is especially relevant to species that are broadcast spawners. Furthermore, fish spawning locations associated with particular ideal habitat conditions, such as moveable gravel sizes for redd construction (Kondolf & Wolman,

1993), or small-scale microhabitat conditions such as depth, velocity, substrate and cover among resident salmonids (Lewis, 1969; Shirvell & Dungey, 1983), therefore have the potential to change alongside the shifting morphological and hydrological conditions of the river they inhabit.

As rivers go through their seasonal cycle, and shift over time, so too may the habitats they create. This may result in shifting spawning locations or timings of fish species that prefer to spawn under specific environmental conditions (e.g., Bartoň et al., 2022). The duration and onset of high water-discharge as a result of seasonality shifts, or anthropogenic alterations by mechanisms such as dams, have been found to alter the reproductive success of spawners with both short (such as broadcast spawners), and long-term (such as bluegill (*Lepomis macrochirus*) that spawn over the course of four months) spawning duration (Craven et al., 2010). Changes in hydrology can affect sediment transport and deposition within the river, influencing available spawning substrates for species that require specific substrate-qualities, such as salmonids (Lisle & Hilton, 1992; Nelson et al., 2010). Some species such as sturgeon, have been found to spawn within specific velocity (Paragamian et al., 2009; Parsley et al., 1993), and depth ranges (Hatin et al., 2002; Paragamian et al., 2009; Wyman et al., 2018), which are subject to change with shifting hydrology, and therefore, may influence where in the river they choose to spawn.

While identifying spawning locations and associated habitat usages may be challenging for some fish species that occupy riverine environments, there are technologies and strategies that can be implemented to aid in the task. Salmonid redds have been identified by visually counting them from boats, manned helicopters, or drones (Gallagher et al., 2007; Ponsioen et al., 2023), while Atlantic cod (*Gadus morhua*) have had spawning habitats identified using remotely operated vehicles (ROV) and hydroacoustic devices such as dual frequency imaging sonar (DIDSON; Grabowski et al., 2012). Other tools that have been successful at identifying spawning areas and associated habitat usage include, but are not limited to, strategies such as telemetry (Brownscombe et al., 2022; Luczkovich et al., 2008), and egg mats (Chiotti et al., 2008; Prichard et al., 2017). The choice of sampling strategy implemented is often dependent on the spawning method used by the species (e.g. nest-building or broadcast spawning), and the environment they live in. Regardless, careful consideration of the information

provided by any particular monitoring program should be evaluated to ensure the spawning strategy is identified as quickly and accurately as possible.

In this study, simulation and in-situ experimentation is used to evaluate egg mat data as a means of determining the environmental variables that drive spawning site selection for Nechako white sturgeon. To help address the key uncertainties of where sturgeon spawn and the habitats they choose to spawn in, this study tackles two major objectives. The first objective is to interpret what the number of embryos on an egg mat tell researchers about where a sturgeon spawned. The second objective is to determine whether egg mat data can be utilized to identify what environmental variables driver Nechako white sturgeon spawning site selection.

## 2.1.1. Study background

The Nechako River extends approximately 240 km, beginning at the Kenney Dam, and ending at its confluence with the Upper Fraser River in Prince George, BC. (Figure 1). Since the Kenney Dam was constructed in 1952, the river's hydrology has been regulated, resulting in flows being reduced to approximately half of their pre-regulated condition in the Vanderhoof area, where the only known spawning reach for Nechako white sturgeon exists (NHC, 2003). The hydrological and morphological deviances of the river from that of its historic norm has caused complications for the Nechako white sturgeon that reside there (McAdam et al., 2005), with it being listed as endangered under the Species at Risk Act (SARA) in 2006 (Fisheries & Oceans Canada, 2014), which prohibits the fishing, harvesting, or killing of the species.

Population decline of Nechako white sturgeon was first identified in the year 2000 after a study estimated the population size to be 571 fish (RL&L Environmental Services, Ltd., 2000), ultimately leading to the population being listed as endangered (Fisheries & Oceans Canada, 2014). The mechanism behind the population decline has been identified as recruitment failure, likely resulting from the loss of larval habitat through the process of interstitial infilling, whereby fine sediments settle and fill the small gaps between substrates (known as interstitial spaces; McAdam, 2012). The precise reason behind Nechako white sturgeon population decline is still unproven, though the cause of interstitial infilling in the Nechako has been suggested to be that of a "sediment wave" that resulted from the 1961 upstream channel avulsion near Cheslatta Falls (McAdam et

al., 2005), which resulted in between 0.4 to 0.5 million cubic meters of sediment being added to the Nechako River (NHC and McAdam, 2003). It has been hypothesized that combined with higher flows in 1964 and 1967, the sediment moved downstream from the avulsion area and arrived within the Vanderhoof spawning reach between 1966 and 1973, which coincides with the rapid decline in recruitment beginning in 1967 (McAdam et al., 2005).

To address the concern of recruitment failure for the species, habitat remediation and population supplementation programs have been initiated. Restoration efforts to circumvent interstitial infilling include providing clean gravel pads (NHC, 2012), and physically cleaning substrates (NHC, 2016; NHC, 2021) to promote larval sturgeon survival (McAdam et al., 2018). Additionally, the Nechako White Sturgeon Conservation Center (NWSCC) was created as a hatchery to back-fill gaps in the age-structure, and ensure hatchery-reared larval sturgeon survived to their first year or two of life. Despite the restorative efforts to improve the spawning grounds, the longevity of these remediation projects is compromised so long as substrate infilling continues to affect the area (McAdam et al., 2018). Further, while the conservation hatchery has led to successful recruitment of juveniles, it is not seen as a permanent solution.

Specific spawning sites of Nechako white sturgeon are currently unidentified on a fine scale. Egg mat monitoring has been used to determine that Nechako white sturgeon spawn between May and July every year in a 3.4 km spawning reach within the district of Vanderhoof, BC, yet it remains unknown where, specifically (within tens of meters), spawning sites exist. Furthermore, it is unknown what habitat characteristics they choose to spawn based off of. Environmental variables underpinning spawning site selection for other sturgeon populations and species include: spawning based on preferred sediment at specific locations (Fischer et al., 2018), at specific velocity (Paragamian et al., 2009; Parsley et al., 1993) or depth ranges (Hatin et al. 2002, Paragamian et al.2009; Wyman et al., 2018), or at a combination of deep pools with fast water (McDonald et al., 2010; Paragamian et al., 2002). Given sturgeon are broadcast spawners that occupy dynamic riverine environments adds layers of complexity to identifying Nechako white sturgeon spawning locations, given that embryos may distribute away from the exact location in which they were spawned, and fine-scale spawning sites cannot be identified visually due to water turbidity in the Nechako during the months of spawning.

Egg mats have been used in the Nechako River since 2004 for the dual purpose of collecting wild-spawned embryos to raise in the hatchery (as of 2015), and to accumulate information of relative captures across a gradient of locations and river conditions (e.g., depth and velocity). It is the hope of researchers that the historic egg mat data collected may be opportunistically used in identifying the conditions favoured by sturgeon to spawn at a fine-scale, in order to consequentially be able to identify areas that are likely candidates for habitat restoration. This fine-scale information would be beneficial to informing targeted habitat restoration efforts to particular areas, so expensive large-scale efforts would no longer necessarily be required.

## 2.2. Methods

This study uses a combination of field experimentation and modeling strategies to determine whether historic egg mat data can be opportunistically used to determine what environmental variables are important in driving sturgeon spawning site selection (Appendix Figure A.1). There has been a long-standing assumption around egg mat collection data that more embryos caught on an egg mat indicates that egg mats were closer in proximity to spawning sites, yet parameters around this assumption are currently unidentified. We therefore begin by performing a field experiment to determine what proportion of eggs are expected to be caught by egg mats at distances downstream from spawning sites, and obtain parameters around how good substrates and egg mats are at catching embryos in both remediated (cleaned), and natural (uncleaned) environments. We then use these parameters to inform simulation models.

Simulation models involve simulating sturgeon choosing spawning sites based on environmental variables, their embryos being released and distributing downstream according to the hydrology of the river at the time, and their embryos being captured by egg mats arrayed throughout the 3.4km stretch of river Nechako white sturgeon are known to spawn in. The results of the simulated egg mat data are then run through estimation models to predict, based on the simulated egg mat capture data, whether spawning is likely to have happened at the location of egg mat captures. Simulation and estimation model results were then compared to see if estimation models could accurately predict what environmental variables were used to simulate sturgeon spawning site selection, based on where sturgeon were predicted to have spawned

given simulated egg mat data, and the associated environmental variables experienced at those sites.

## 2.2.1. Egg Drift Experiment

In the Nechako white sturgeon Spawning reach in Vanderhoof, BC, one section of a side-channel, measuring 1 m wide by 14.8 m long, was mechanically "cleaned". The cleaning process used a device that physically sorted fine sediments, so substrates such as gravel and cobble sat atop sandy substrates. After the cleaning was performed, an equally sized uncleaned section was erected beside it, resulting in side-by-side 'clean' and 'unclean' lane-ways of equal dimension. Five 0.8 m x 0.8 m egg mats with clean furnace-fleece material were placed in the center of each lane-way. The beginning of each egg mat was placed at 1.70, 2.89, 4.91, 8.35 and 14.20 m downstream from the release site to account for the expected exponential decay of embryo captures. Two drift nets with removable codends were installed one above the other at the end of each experimental lane (14.8 m downstream of the release site), to block the entire water column at the end of each lane-way. The nets spanned the width of each lane, and reached from the substrate to above the water in an attempt to ensure that any embryos still in the water column at the end of the lane would be caught within the nets (Figure 2).

Approximately 1,000 embryos were released in both laneways using PVC tubes suspended 0.3 m from the substrate. It is unknown where in the water column white sturgeon release eggs, so 0.3 m was chosen to be consistent with the hypothesis that egg release occurs near the bottom (Bruch and Binkowski, 2002; Golder Associates Ltd., 2008; Hildebrand et al., 2016). Broodstock-collected eggs from three females were used over the course of the experiment, and were counted volumetrically (where, on average of 31.6 mL equated to 1000 eggs), fertilized over the span of 1:15 minutes (using the combined sperm of three broodstock males that all had sperm motility levels ranging between 75-100%), and released down the PVC tubes. This procedure accounted for the time needed to initiate adhesion in embryos, which begins after fertilization (Cherr & Clark, 1985), and was noticed to onset within the 1:15 minute fertilization period. Egg mats and drift nets were removed from the river ten minutes after each embryo release, starting with the drift nets before working upstream from the most downstream mat. Embryos from each mat and drift net were then manually counted and

removed. Six release replicates were performed in the same day under approximately the same river conditions

Embryo captures on egg mats in clean and unclean habitat was assumed Poisson distributed:

(1)      $C_{t,l,i} \sim Poisson(\hat{p}_{t,l}, \widehat{N}_{(0)t,i})$

where $C_{t,l,i}$ is the number of embryos captured in $t$ treatment (clean or unclean), on $l$ capture location, at $i$ replicate. $\widehat{N}_{(0)t,i}$ is the number of embryos released for each treatment, and $\hat{p}_{t,l}$ is the predicted probability of capturing an embryo at a particular site, given the treatment.

The proportion of embryos remaining in the water column ($\hat{r}_{t,l}$) at location $l$ downstream was assumed to decline exponentially at a rate based on the cumulative types of substrates encountered (clean, unclean, mats) between that location and the release site:

(2)      $\hat{r}_{t,l} = \exp\left[-\hat{q}_{(s)t}(D_l - n_l L) + \hat{q}_{(m)t}(n_l - 1)\right]$

where $\hat{q}_{(s)t}$ is the capture rate of cleaned or uncleaned substrates and $\hat{q}_{(m)t}$ is the capture rate of all mats encountered before the current location. The coefficient $\hat{q}_{(s)t}$ is multiplied by the cumulative distance of habitat, less the distance covered with mats, where $D_l$ is the downstream extent of egg mat $l$, $n_l$ is an index representing the $n^{th}$ egg mat downstream of the release location, and $L$ is the length of the egg mat (0.8 m). This formula accounts for losses due to substrate (cleaned or uncleaned) and any mats that embryos have drifted past prior to the start of capture location $l$.

Capture probability of each mat was calculated as the proportion of embryos in the water column at the leading edge of each mat, multiplied by a finite capture probability:

(3)          $\hat{p}_{t,l} = \hat{r}_{t,l}(1 - e^{-q_{(m)t}})$

Prior probability for number of released embryos in each treatment and replicate were assumed normally distributed with mean and standard deviation based on volumetric

measurements taken at the time of each release. Prior probabilities for all estimated parameters are shown in Table 1.

All calculations were performed in R (4.2.0). JAGS (Just Another Gibbs Sampler; Plummer, 2003) was used to numerically approximate the posterior probability distributions of parameters using sampling Markov Chain Monte Carlo (MCMC) simulation. Posterior distributions were calculated from 10,000 iterations after an initial burnin of 5,000 iterations and further thinned to provide a final sample of 1,000 iterations from each of three MCMC chains. Convergence could not be rejected given visual inspection of MCMC chains and Gelman-rubin convergence diagnostics available in the CODA package of R (Plummer, 2010).

Note that although parameters were estimated for cleaned and uncleaned habitats, cleaned habitats were not considered in the simulation. Therefore, all mention of habitat in the simulation model will assume uncleaned habitat.

## 2.2.2. Egg Capture Simulation

It is unknown what habitat characteristics Nechako white sturgeon look for when choosing a location to spawn. We therefore considered three hypotheses on what environmental variables drive sturgeon spawning site selection in this study: spawning location based on velocity and depth (habitat-based); spawning location based on X-Y position in the river (location-based), and spawning location based on velocity, depth and location (location and habitat-based). Generalized Additive Models (GAMs) were used to generate simulated sturgeon spawning probability in each 5 x 5 m quadrant in the spawning reach. To parameterize these models, egg mat capture data collected from Triton Consulting (Triton, 2004 - 2009; Sykes, 2010), CSTC (unpublished data, 2010 - 2021) and NWSCC (unpublished data, 2017 - 2022) egg mat monitoring programs were fit to GAMs representing the three spawning strategies. Combining these data resulted in 6,414 data points. However, to test these hypotheses, all environmental variables that were sought to be examined needed to have been recorded, therefore only egg mat capture records with velocity, depth, and location were included. Filtering records that contained all three variables resulted in 639 observations (Figure 3).

Egg mat data were analysed using GAMs in the mgcv R package (Wood, 2017). GAMs were chosen for this study as they allow for the fitting of nonlinear functions, and are more flexible than Generalized Linear Models (GLMs). GAMs are the sums of smooth functions, such as splines, and are capable of estimating a large number of parameters using a penalized likelihood (Venables & Dichmont, 2004). Splines are piecewise polynomials that join at points called knots, and while there are many splines to choose from, this study uses two: smooth splines and tensor splines. Smooth splines are capable of capturing non-linear relationships between the response and the predictor variable and are computationally more efficient than tensor splines, though tend to use fewer parameters. Tensor splines allow for more complicated interactions between predictors and the response variable, and are often used when there are multiple predictors that have interactions between them. The more knots in a GAM, the more flexible it has the potential to be, and therefore, the more the model may overfit the data. GAMs compensate for this by penalizing the number of estimated parameters, balancing model fit against overfitting.

Three GAM model structures were used, corresponding to the three spawning strategies:

(4) $$g(C_j) = s(D_j) + s(V_j),$$

(5) $$g(C_j) = t(X_j Y_j),$$

(6) $$g(C_j) = t(X_j Y_j) + s(D_j) + s(V_j),$$

where variables $D_j$ and $V_j$ represent depth and velocity at egg mat $j$, $X_j$ and $Y_j$ represent Easting and Northing of egg mat $j$, and $C_j$ represents the observed embryo catch. Splines include smooth [$s()$] and tensor [$t()$] splines. Models were fit assuming a Poisson likelihood and used a log-link function, represented by g().

Each fitted GAM was used to generate spawning probability in each 5 x 5 m cell in the spawning reach based on appropriate combinations of X-Y location, depth and velocity (Figure 4). These conditions were calculated based on output of the hydrological model in Gauthier-Fauteux (2017). These hydrologic data were calculated based on 18 different discharge levels (48, 78, 125, 175, 225, 275, 325, 375, 425, 460, 475, 525, 575, 625, 675, 725, 775, and 800 $m^3$/s). Different discharges results in a different velocity and

depth for each cell, and different shoreline configuration as the water level rises, leading to different available habitat.

For every simulated year, one of the 18 different discharge levels was randomly selected, which altered the hydrology of the river, and ultimately where sturgeon were more likely to spawn in that year. Predictions from the hydrologic model were used as inputs to each fitted GAM model, which allowed predictions of embryos captures in each cell of the spawning reach. Embryo captures in cell *j* were transformed to spawning probabilities between 0 and 1, by linearly rescaling each value to within the range of all cells, as suggested by Tian et al. (2009):

$$(7) \qquad \hat{p}_j = \frac{\hat{c}_j - min_j(\hat{c}_j)}{max_j(\hat{c}_j) - min_j(\hat{c}_j)}$$

Here, a value of 0 indicates that the location the egg mat was placed in is not predicted to be a site in which sturgeon spawn, while a value of 1 suggests that it is most likely a sturgeon spawning site, and a value of 0.5 signifies a 50% probability that the site will be selected for spawning. It is important to reiterate that this process of converting predicted embryo captures to spawning probabilities is not meant to equate these two processes, but simply to provide a plausible simulation model for generating spawning distribution in the river conditional on which biological process (hydrology, location, or both) is being used to drive spawning site choice by Nechako white sturgeon.

Three egg mat spatial arrangements were selected for simulation that have been utilized by Nechako white sturgeon research groups (Triton, CSTC and NWSCC) over the years: Random, Site-Specific, and Random Groupings (Figure 5). The "Random" array refers to randomly selecting a location from the spawning reach to put a single egg mat down. The "Site-Specific" array involves splitting the spawning reach into ten spatial zones (Figure 6) and then randomly selecting a location from that zone to put a single egg mat down. The third array "Random Groupings" is similar to the "Random" array, but instead of putting down a single egg mat in that location, it puts down two.

Constraints were put on the simulated egg mat distribution to emulate historic Nechako white sturgeon egg mat sampling conditions. First, it was simulated that 40 egg mats were deployed every year to match average annual egg mat deployment between the years 2004 and 2022. Secondly, it was simulated that an egg mat would only be placed

down in a site that had at least 0.3 m of water to reflect research vessels being unable to deploy egg mats in less than 0.3 m of water.

The model assumes 50 spawning pairs per year, where actual spawning sites were generated using a random binomial process with probability equal to the simulated spawning probability across river cells (Eq. 7). An estimated 550 adult Nechako white sturgeon were in the 2022 population (Carruthers et al. in review). Simulating 50 wild spawning pairs per year is therefore consistent with an assumed equal sex ratio where each female spawns every 3-5 years on average (Haxton et al., 2016).

Embryos released at each spawning site were dispersed through the river. It is unknown how many eggs Nechako white sturgeon release in a given spawning event, so at each spawning site, 250,000 eggs were simulated to be released, which is reasonable given that white sturgeon may be capable of spawning upwards of 700,000 eggs (Scott and Crossman, 1973), and Chapman et al. (1996) found that white sturgeon on the Sacramento River produce an average of 203,328 eggs. Embryos were simulated to move downstream to the next 5 x 5 quadrant using a Lagrangian model conditional on the directional velocity generated from the hydrological model of Gauthier-Fauteux (2017). Across fifty time-steps, a proportion of embryos would settle out of the water column as predicted in Eq. 2 based on the habitat of that cell (egg mat or substrate). Remaining embryos would move to surrounding cells according to the direction of water movement in that cell, in each direction, predicted from the hydrological model. Fifty time-steps were chosen as this is consistent with a downstream distance of 250 m, which the experiment (Section 2.1) predicts would result in fewer than 1 spawned embryo still in the water column. Embryos were only able to distribute themselves in water, so cells that were not wetted under particular discharge conditions received no spawned or drifted embryos.

Capture probability of simulated egg mats was determined using the following formula,

(8) $\qquad \hat{p}_j = \hat{E}_j (1 - e^{-q_{(m)}})$

where $\hat{E}_j$ is embryos predicted to be in the water column of cell $j$, $q_{(m)}$ is capture efficiency of egg mats in uncleaned habitat estimated from the egg drift experiment (Section 2.1).

Egg mat captures were a binomial random variable based on the probability of capture (Eq. 8). These egg mat capture data, simulated over nineteen years of randomly selected discharges, were used as 'fake' data to fit GAMs intended to make predictions of spawning probabilities.

It was necessary to make assumptions for the purpose of the simulation model, as parameters on Nechako white sturgeon spawning remain unknown. The physical assumptions involved: the habitat of the river (the river was assumed to be unclean, and the hydrology was assumed to be that of one of the 18 different discharges we had simulation data for), the depth in which egg mats could be deployed (depths greater than 0.3 m), and the number of egg mats deployed every year at the time of spawning (40). The biological assumptions included: the amount of spawning pairs that spawned every year (50), the depth sturgeon would spawn in (depths greater than 0.3 m), the timing of spawning (spawning was simulated to occur at the same time for all pairs, and would happen once a year), the fecundity of females (250,000 embryos released at each spawning site), and the adhesion of embryos (all embryos were considered to be as adhesive as they were after having been fertilized for 1:15 minutes during the experiment). While all of these assumptions affect the results of this study, female fecundity, the number of egg mats deployed are expected to affect results the most. By increasing the number of embryos released at spawning sites or the number of egg mats deployed is anticipated to result in more embryos being caught by egg mats.

## 2.2.3. Estimation Model Analysis

The purpose of the estimation models is to evaluate different hypotheses of site selection by spawning Nechako white sturgeon. Three GAMs were created to estimate the probability of spawning happening at the site of each egg mat, given the catches of egg mats. These probabilities were used to determine whether egg mat data could accurately predict relative spawning probabilities in different river sites, and predict the spawning strategy sturgeon used at those locations, given there was a specific spawning strategy used to generate the data. The GAM models used to evaluate the three hypotheses for how sturgeon choose spawning habitats reflect the same models used to generate spawning probability:

$$(9) \qquad g(C_j) = s(D_j) + s(V_j),$$

$$(10) \qquad g(C_j) = t(x_j, y_j),$$

$$(11) \qquad g(C_j) = t(x_j, y_j) + s(D_j) + s(V_j),$$

which represent the three hypotheses where spawning sites are chosen based on: depth and velocity; location; or depth, velocity, and location, respectively. This model was executed using the mgcv package in R (Wood, 2017), using a Poisson distribution, and the method "REML".

Estimation models predicted the number of embryos caught on an egg mat. To relate the number of embryos on an egg mat to where a sturgeon actually spawned, it was assumed that an egg mat would catch more embryos the closer it was to a spawning event. This logic is consistent with the premise of using egg mats to determine spawning locations, which is the basis of this study. Therefore, predicting how many embryos are caught on an egg mat, is also predicting the probability of spawning at that site. Estimated predictions were rescaled using min-max scaling, as with Eq. 7, above.

Nineteen years' worth of egg mat data were simulated and run for 150 iterations. Additional iterations (>150) resulted in no change to median Root Mean Square Error (RMSE) between simulated and estimated spawning probability values (Appendix Figure A.2). Models were ranked according to their calculated Akaike Information Criteria values (AIC). For each of the 150 iterations, models were ranked and the mean proportion of iterations in which each model was top ranked was calculated. Visual comparisons of the mismatch between where sturgeon were simulated to have spawned and where they were estimated to have spawned were performed to determine plausible mechanisms behind any discrepancies.

## 2.3. Results

### 2.3.1. Egg Drift Experiment Results

Embryos released in the field experiment show a consistent exponential decay pattern that helps understand the extent to which spawned embryos drift downstream. Posterior checks of model estimates against data suggest the model is able to capture

the overall decay process of embryos drifting downstream as they cumulatively adhere to either substrate or egg mats (Figure 7).

The extent of downstream drift is less in clean substrate, because embryos have lower retention in unclean habitat. This is validated by a mean instantaneous capture probability of clean substrate ($\hat{q}_{(s)t=clean} = 0.17$) being twice that in unclean substrate ($\hat{q}_{(s)t=unclean} = 0.07$; Figure 8). Instantaneous capture probability of clean substrate also appears to be less variable with a coefficient of variation (CV) of 0.12 relative to unclean substrate, which has CV of 0.18. Capture efficiency of mats in clean and unclean habitats are not appreciably different, suggesting substrate type does not affect adhesion of embryos on egg mats (Figure 8).

Model predictions using egg drift experiment data reveal that egg mats on uncleaned substrate are predicted catch embryos further downstream than egg mats on cleaned substrate (Figure 9). This reflects the lower adhesion in unclean substrates, meaning more embryos remain in the water column (Figure 9). Therefore, an egg mat set 20 m downstream is likely to capture 1% and 7% of released embryos in clean and unclean substrate, respectively.

Regarding substrate retention of embryos, models predict that 95% of embryos are retained within the fist 46 m in unclean environments, and within the first 18 m in clean environments. These findings must be caveated by reiterating that eggs had been fertilized for 1:15 minutes prior to being released down PVC tubes, and adhesion had already been noted to onset in embryos prior to release, which, under natural spawning conditions, may not be the case.

## 2.3.2. Egg Capture Simulation Results

Embryo releases were replicated using the simulation model and showed different distribution patterns throughout the spawning reach, depending on the environmental variables driving spawning site selection (Figure 10). Embryos had a tendency to be distributed into particular locations, as directed by where the water was channeled. Captures were consistently found in offset locations from sturgeon spawning sites, and were inaccurate at predicting fine-scale spawning locations (Figure 11). These

areas tend to be specific locations that experience high velocities and depth, such as the center of the river (the channel thalweg; Figure 12).

Model ranking by AIC does not consistently select the hypothesis used to determine simulated spawning locations by Nechako white sturgeon (Table 2). Most commonly selected models are those that include depth, velocity, and location regardless of the spawning strategy used to simulate spawning (Appendix Table A.1, Table A.2, Table A.3). While the model occasionally selects the correct environmental variables used to simulate sturgeon spawning site selection that resulted in the simulated egg mat data, the exact fine-scale spawning locations are not correctly identified.

## 2.4. Discussion

This study suggests historic egg mat data alone cannot be used to establish what environmental variables drive Nechako white sturgeon spawning site selection on a fine scale. The simulation presented in this study requires the translation of embryos densities into spawning probabilities, under the assumption that more embryos captured on an egg mat implies it was closer in proximity to the point of spawning. However, given sturgeon are broadcast spawners, embryos are prone to drifting where water is channeled: often to particular locations, such as the center of the river, where high velocities and depths are experienced. Velocity and depth are important aspects to two of the hypotheses evaluated in this study, though do not necessarily correspond with the environmental variables that underpinned simulated sturgeon spawning site selection. Therefore, this simulation-evaluation study demonstrates that data consistent with what is available would nearly always support a hypothesis that depth and velocity are important factors, regardless of whether that is true. Therefore, egg mat data is ineffective at predicting relative spawning probabilities of different habitats, and cannot discern the environmental cues that sturgeon use in selecting fine-scale spawning sites. This indicates that while egg mats may be beneficial to determining large-scale extents of spawning reaches, the total number of embryos on an egg mat in flowing rivers is a poor proxy for where sturgeon actually spawn on a finer scale.

While identifying spawning sites and their associated habitat characteristics may be important for the recovery of some species at risk, it is not possible using egg mat data alone when situated in riverine environments. While egg mats have been reportedly

successful in aiding to identify or confirm the extents and habitat associations of lake sturgeon (e.g. Chiotti et al., 2008; Fischer et al., 2018; Smith et al., 2017), green sturgeon (e.g. Poytress et al., 2015), and white sturgeon (e.g. Paragamian et al., 2009; Parsley & Kappenman, 2000) spawning reaches, our study suggests that fine-scale detection of white sturgeon spawning sites in rivers is misleading when utilizing only historic egg mat data. This is attributed to the fact that high egg mat captures of embryos reflect where they were distributed according to the hydrology of the river, which is not necessarily where spawning occured. Many species of fish depend on specific habitat types and environmental conditions for their survival during various life stages (Bjornn and Reiser, 1991; Rosenfeld, 2003). In these situations, accurate information on habitat use and dependencies are vital to informing realistic restoration goals for the species (Ehrenfeld, 2000), in order to improve conditions and bolster species recovery.

Given the complexity of the rivers in which they reproduce, simulating fish spawning and the conditions in which they spawn is challenging. Water flows will push embryos downstream of spawning sites, as has been demonstrated here and elsewhere (Garcia et al., 2015; Li et al., 2023). This disassociation between sturgeon spawning and embryo capture sites complicates the identification of fine-scale spawning locations based on where embryos are found, as is the case in this study. Furthermore, while flow variability in rivers is an important driver of ecosystem processes (Naiman et al., 2008), the variability in discharge levels and flow between years makes it difficult to predict how embryos are likely to move and distribute in an upcoming spawning season.

Although historic egg mat data alone is unable to accurately determine the environmental cues guiding Nechako white sturgeon spawning site selection, they are capable at achieving other goals. Egg mats seem capable at performing other tasks on their own with respect to sturgeon monitoring, specifically: detecting whether a spawning event has occurred upstream of an egg mat, identifying the approximate timing of the event, and capturing wild-spawned embryos. Despite fish research groups utilizing egg mats for all of these purposes in river settings (e.g., Miller et al., 2011), it has been found that utilizing only egg mat data to determine spawn timing in some species is not always sufficient compared to other methods (Irvine et al., 2017). Despite the limitations egg mat monitoring has, it is often coupled with more active sampling techniques that could be used to answer the questions egg mats, alone, cannot.

While egg mats, on their own, are not useful for identifying the environmental variable driving white sturgeon spawning site selection in riverine systems, other technologies could be employed to achieve the goal. In the case of Nechako white sturgeon, adapting the already existing telemetry programs may potentially be a method to discover fine-scale sturgeon spawning locations in the future. It may be possible to identify sturgeon spawning locations by strategically building an array of acoustic telemetry stations throughout the spawning reach to pinpoint areas of aggregation, and habitat usage as has been done for other fish species (Binder et al., 2016; Hayden et al., 2018; Luczkovich et al., 2008), and for other populations of sturgeon (Auer and Baker, 2007; Colborne et al., 2019; Golder Associates Ltd, 2009; Pendleton et al., 2019; Vine et al., 2019). However, despite the promise these telemetry programs may show, they are expensive and should consider the challenges associated with telemetry (Brownscombe et al., 2022). Egg mats could then be used in tandem with these methods to confirm spawning occurred upstream, and to capture wild-spawned embryos downstream of where adult sturgeon are found to be holding during the spawning season. However, it must be cautioned that the hydrology of the river will still need to be considered as embryos will be directed where the water in the river is channeled.

The manor in which historic egg mat data was collected posed challenges to this study. Of all the egg mat data that had been historically collected, only 10% had all the variables recorded that were of interest for this study (velocity, depth, and location), and therefore most of the recorded data (the remaining 90%) was not usable in this study's analysis. An additional reason the data used in this study was such a small proportion of what was historically recorded was due to the inconsistent recording of environmental variables among research groups. For example, the variable of velocity was measured several different ways by Triton, CSTC, and NWSCC, with those ways being: "velocity", "velocity at 50 cm", "surface velocity", "deployment velocity", and "retrieval velocity". These different forms of the same variable were not all able to be compiled together as they are not all compatible, and so further limited the amount of data that was usable for this study. It is therefore advised that when collecting data in the future, for the egg mat program or otherwise, that one or two clearly defined categories of each variable are selected and consistently sampled at each site to allow for more data points to be used when answering future research questions that relate to environmental variables.

Given the limitations of the field-based egg drift experiment, there are implications to the extremities of which embryos were simulated to have dispersed, that should be taken into consideration. One drawback is that eggs were assumed to be adhesive from the moment they were released into the water column, despite the fact that eggs are only adhesive after they are fertilized (Cherr & Clark, 1985). Given the fastest velocities simulated in the river as part of the hydrological models' output were 2.83 m/s, and maintaining the assumption from the egg drift experiment that spawning occurs at 0.3 m from the bottom of the river, Nechako white sturgeon eggs are expected to travel 212.3 m downstream, at most, before becoming adhesive. This may be less than the several hundred meters suggested for Pallid Sturgeon (Kimberly et al., 2020), but still implies that embryos would actually be caught further away from where they were simulated in the model. Another limitation is that parameters on substrates and egg mat catch rates were conducted over a single velocity; therefore, it is unknown how velocity affects embryos drift rates. The simulation model assumes drift distances and associated catch rates of egg mats remain the same for all velocities. If this is not true, it implies that in higher water velocities than experienced in the field experiment (which occurred 89.3% of the time according to simulated hydrological data), the model underestimates embryo dispersion, and in lower velocities (which occurred 10.7 % of the time), it overestimates.

While there are benefits to using historic data for novel purposes, the way data is collected, and how the sampling strategy was designed to collect the data, does not always support its use in answering retrospectively considered management questions. It would have been advantageous to opportunistically utilize the 19+ years of data collected as part of the egg mat program to determine where fine-scale spawning sites are situated within the 3.4 km spawning reach, and what environmental variables drive these decisions, but the program was not designed in a way that allows researchers to answer this question. The results from this study suggest that other methods and programs will need to be implemented or altered in order to accomplish this objective. Although additional parameters surrounding white sturgeon spawning behaviours may make simulation models more realistic to current conditions, (such as parameters on how many eggs are spawned by a single female at a time, what depth sturgeon spawn eggs at, and how egg mat catch rates of embryos vary under different velocities), this study demonstrates that the way egg mats have been sampled historically cannot be accurately used to determine where sturgeon are spawning on a fine-scale.

Future work in this area could involve building on the egg mat simulation model, or turning to other technologies to determine fine-scale spawning locations of white sturgeon in future years. Further modeling work could involve performing a power analysis to determine the necessary egg mat densities required to achieve a fine-scale precision of spawning site detection within a specific time frame that is dependent on how soon managers want answers to this question. Considering the urgency surrounding Nechako white sturgeon recovery, fine-scale precision may be needed sooner than strategic egg mat sampling may provide. Therefore, alternative programs that utilize other technologies should be considered to achieve this objective in a shorter time frame, in order to begin targeting the right habitats for restoration. Should the egg mat program continue with the focus of detecting fine-scale spawning locations, researchers will need to consistently sample the key environmental variables suspected to be driving spawning habitat site selection at the location egg mats are deployed (for example, velocity, depth, substrate composition, etc.) in order to be useful in future analyses. Regardless, managers should consider historic egg mat data as a sunk cost, and moving forward will need to weigh the opportunity cost of continuing to sample using egg mats in these manners, which this study suggests have limited abilities in locating sturgeon spawning sites on a fine-scale.

In conclusion, while improvements could be made to the egg mat program and model procedures, nothing detracts from the main findings of this study: that egg mat data alone cannot be used in determining what strategy white sturgeon use to spawn, or to identify where they will spawn, given river hydrology. Despite the recovery of species at risk being costly (Schneider, 2023; Wilcove & Chen, 1998), supporting critical life stages (Hardy and Litvak 2004), can be accomplished by improving our understanding of these stages. This in turn requires monitoring programs that inform this understanding (Hale et al., 2020; Suding, 2011). In the future, it is advised that as questions surrounding Nechako white sturgeon behaviour and habitat usage become integral in their management, monitoring programs and their affiliated methods are specifically curated to quantitatively tackle the task.

# Chapter 3.

# Outlook

This study demonstrates the limitations of egg mats for use in fine-scale detection of fish spawning locations in dynamic environments, such as rivers. Results increase our understanding of the efficacy of egg mats as a tool for monitoring sturgeon spawning behaviour in rivers. It would have been convenient to use data from the egg mat program to determine habitat characteristics involved in fine-scale sturgeon spawning site selection, but this study reveals such an analysis would have provided misleading conclusions. Our study shows that data consistent with what is available would nearly always support a hypothesis that depth and velocity are important variables, regardless of whether or not it is actually the case. Another monitoring program will need to be implemented or adjusted to target the specific question of where, sturgeon are spawning in the river on a fine scale, and what environmental factors play a part in that decision.

Egg mats continue to play a vital role in Nechako white sturgeon recovery, as they provide a mechanism of capturing wild-spawned embryos. These wild-spawned embryos augment genetic diversity of hatchery-released juveniles, which is important to the success of supplementation programs (Thorstensen et al., 2019), like the NWSCC. Although egg mats have been shown in this study to be ineffective at catching large portions of embryos that may be beneficial to improving the genetics of supplemented juveniles released from the NWSCC, when it comes to sturgeon embryo collection, egg mats appear to be the preferred strategy of research groups as they can be utilized in many spatial arrays, and work to passively collect embryos. Aside from the use of egg mats in embryos collection and embryos density estimations, other methods have been implemented, such as plankton nets, bottom trawls, egg trays, diver-collected quadrant samples, drift nets, and kick nets (Haxton et al., 2023; McCabe and Beckman, 1990; Nichols et al., 2003). The appeal of egg mats compared to these other strategies is the ability to collect embryos from egg mats with relative ease, while keeping eggs viable and relatively free of damage.

The recovery of Nechako white sturgeon will be determined by how well early life stages can be supported to overcome the point of their recruitment failure. While identifying fine-scale sturgeon spawning locations would serve as a useful recovery factor with respect to determining where, precisely, to concentrate habitat restoration efforts, egg mats are not the tool for the task. In the meantime, more broad habitat restoration programs may have to suffice with respect to substrate quality that is conducive to larval sturgeon survival. A current broad-scale restoration proposal involves excavating a sediment trap within the spawning reach to alleviate a portion of the riverbed that may be more prone to bedload sediment transport, while additionally, adding gravel to targeted sections of the spawning reach (NHC, 2023). Gravel additions must take into consideration the quantity necessary to provide adequate larval habitat (e.g., McManamay et al., 2010), and, as with any physical alteration to the environment, these restoration efforts require careful consideration prior to their implementation, as they have the potential to make hydrological and morphological changes to the river (Kondolf, 1998; Wheaton et al., 2004).

As answers surrounding Nechako white sturgeon behaviour become more and more necessary to their recovery, programs should be specifically designed to get measurable results. Caution should be exercised when using existing datasets to answer important management questions. These data were not collected for this purpose and resultant mismatches may lead to false interpretation. Instead, the success of the monitoring programs will depend on them having a thorough study design (Lindenmayer & Likens, 2010), which monitors and measures attributes pertaining to the objectives of the program in a standardized and consistent manner (Kondolf, 1998; Reynolds et al., 2016; Shafroth et al., 2008; Vos et al., 2000). The sampling techniques used for these programs will then need to be thoughtfully deliberated to weigh the challenges they bring and their effectiveness at answering the questions posed (Sharma, 2017). Moving forward, further work is needed to identify specific spawning sites, and the environmental qualities in which Nechako white sturgeon choose to spawn, in order to effectively target restoration efforts to improve larval survival, and overcome recruitment failure.

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# Tables and Figures

## Tables

**Table 1**    Prior probabilities of estimated parameters used in the egg depletion model. *N* denotes a normal distribution, and *LN* denotes a lognormal distribution.

| Parameter | Description | Prior probability |
|---|---|---|
| $N(0)$ | Initial release abundance | *N*(1015,185) |
| $q_{(s)t=clean}$ | Instantaneous catchability of clean substrate ($m^{-1}$) | *LN*(0,1) |
| $q_{(s)t=unclean}$ | Instantaneous catchability of unclean substrate ($m^{-1}$) | *LN*(0,1) |
| $q_{(m)t=clean}$ | Instantaneous catchability of egg mat in clean substrate | *LN*(0,1) |
| $q_{(m)t=unclean}$ | Instantaneous catchability of egg mats in unclean substrate | *LN*(0,1) |

**Table 2**      Contingency table relating the percent of 150 simulation-estimation iterations where each simulated sampling strategy was selected as the most parsimonious model through AIC. Bolded values are the strategies selected as the best fitting model whereas shaded values are the simulated strategy that was actually used.

| Estimation model (GAM) | Hypothesized habitat characteristics simulated to drive sturgeon spawning site selection | | |
|---|---|---|---|
| | Velocity & depth | Location | Velocity, depth & location |
| Random egg mat sampling strategy | | | |
| Velocity & depth | 38.7 % | 0.0 % | 0.0 % |
| Location | 0.0 % | 0.0 % | 0.0 % |
| Velocity, depth & location | **61.3 %** | **100.0 %** | **100.0 %** |
| Site-specific egg mat sampling strategy | | | |
| Velocity & depth | 27.3 % | 0.7 % | 0.7 % |
| Location | 0.0 % | 1.3 % | 0.0 % |
| Velocity, depth & location | **72.7 %** | **98.0 %** | **99.3 %** |
| Random groupings egg mat sampling strategy | | | |
| Velocity & depth | 22.0 % | 0.7 % | 0.7 % |
| Location | 0.0 % | 2.0 % | 0.0 % |
| Velocity, depth & location | **78.0 %** | **97.3 %** | **99.3 %** |

# Figures
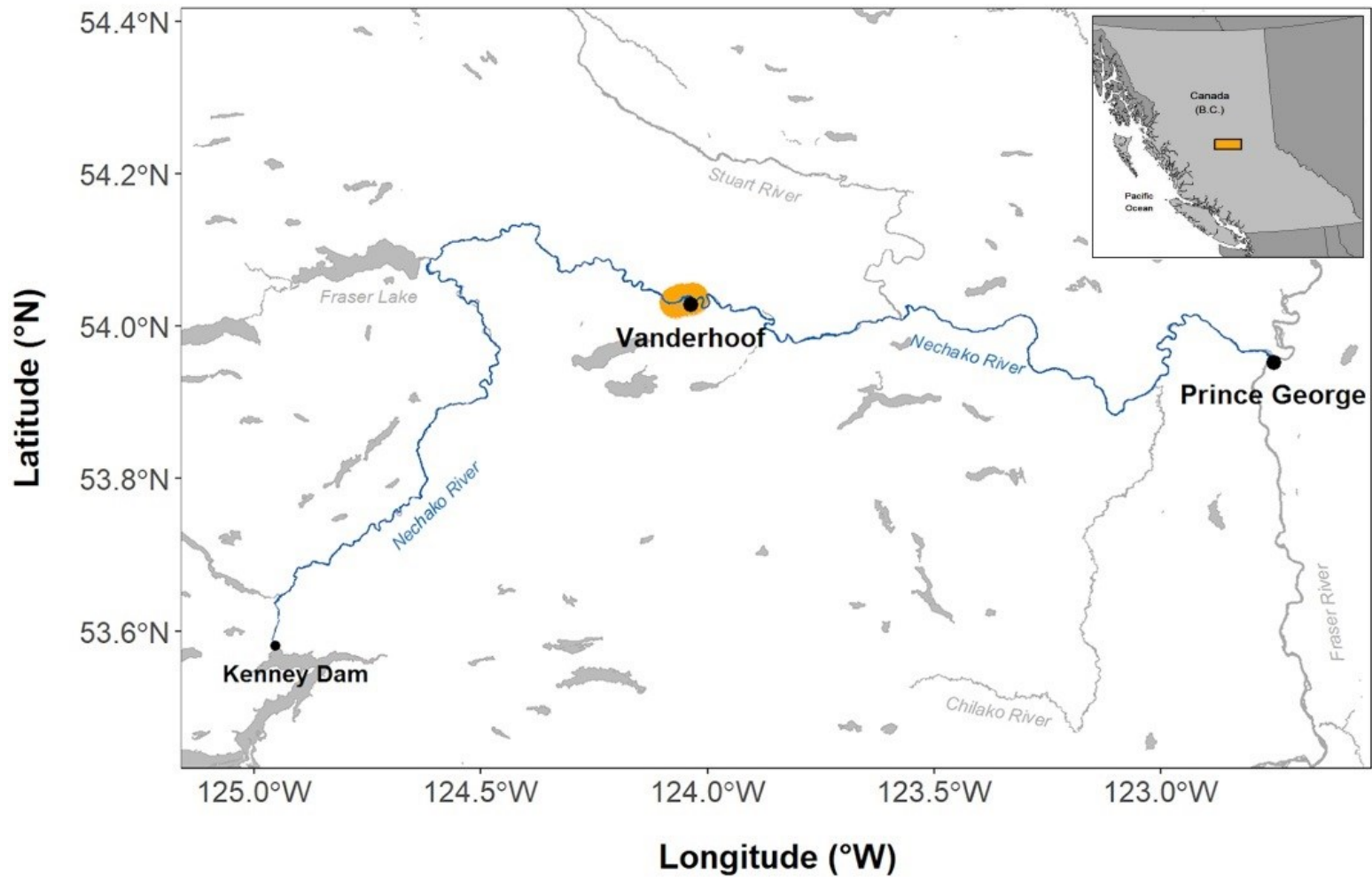
**Figure 1**     A Map of the Nechako River from where it begins at the Kenney Dam, to where it ends at the Nechako River-Upper Fraser River confluence in Prince George. The orange box on the map of British Columbia (top right) indicates the orientation of the main situated within the province, and the orange shaded area (above) indicates the section of the river that is the only known spawning reach for Nechako white sturgeon.
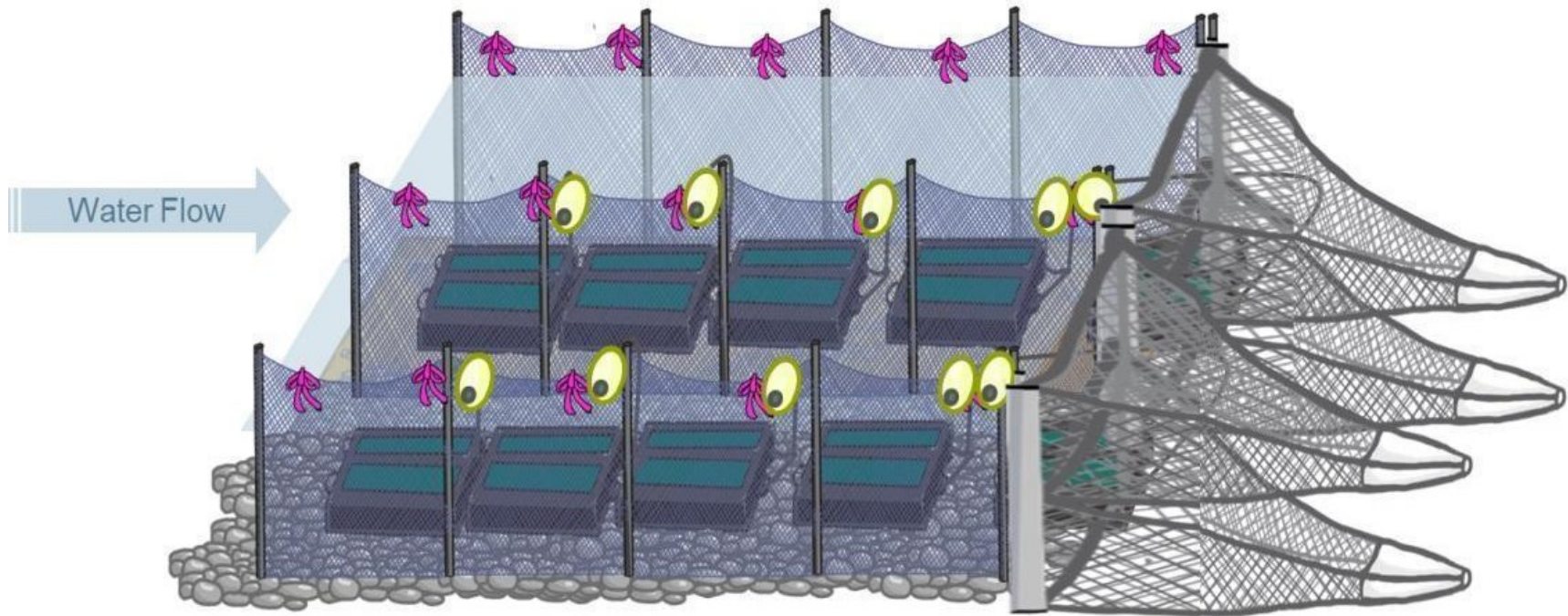
**Figure 2**    A schematic of the field experiment set-up. Each laneway measured 1 m wide by 14.8 m long, with driftnets and detatchable codends placed at the 14.8 m mark. Five 0.8 x 0.8 m egg mats were placed at 1.70, 2.89, 4.91, 8.35 and 14.20 m downstream from the start of each laneway.
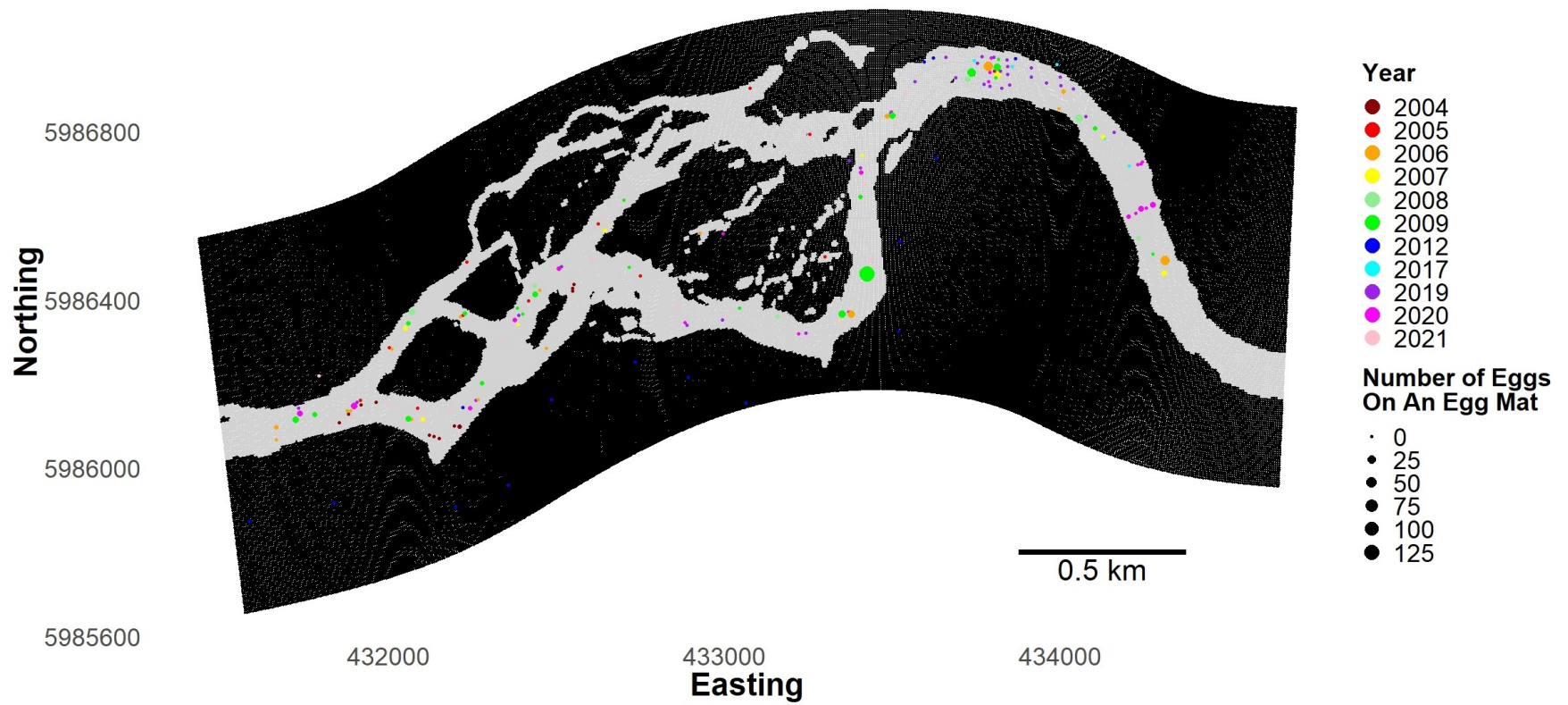
**Figure 3**     Location of 639 observations used to calculate spawning probabilities throughout the 3.4 km spawning reach. The gray section denotes the extent of the river at 48 m³/s discharge, which may not reflect conditions under which egg mats were set; the size of points reflect how many eggs were caught on each egg mat.
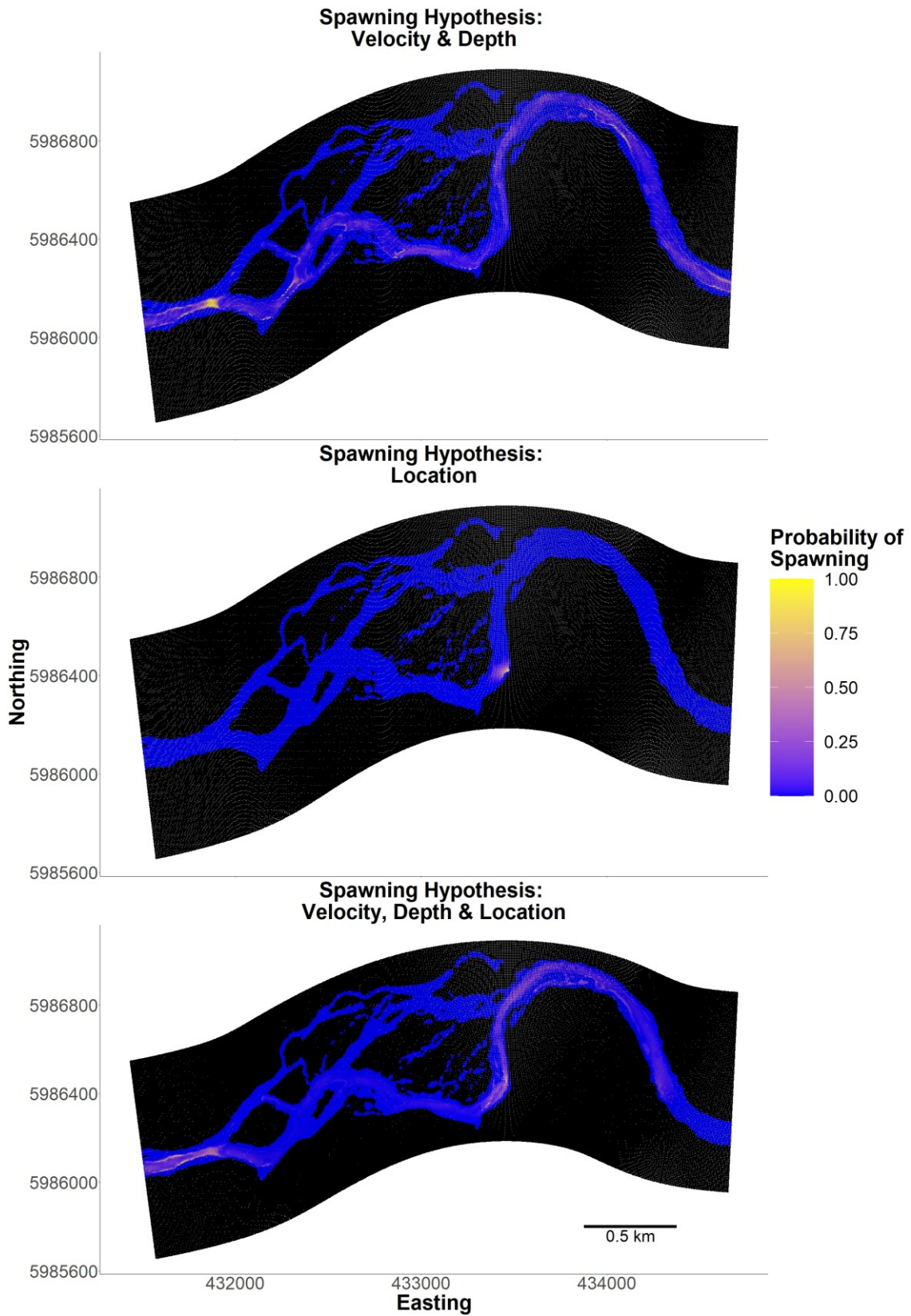
**Figure 4**     The probability of spawning throughout the spawning reach for each spawning hypothesis at a river discharge rate of 48 m³/s.
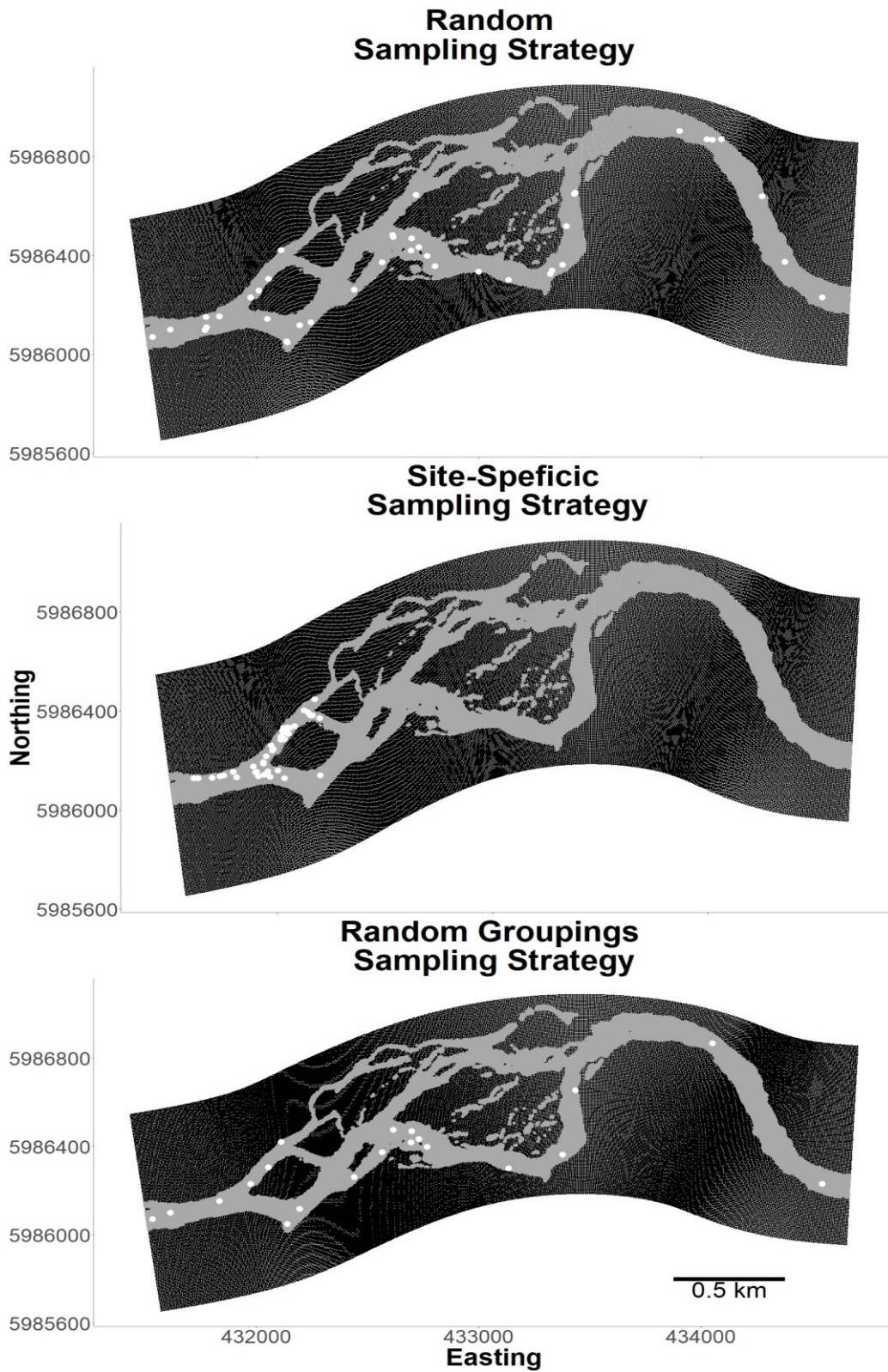
**Figure 5**      An example of how each egg mat sampling array might look for a single year with 40 egg mats placed for each array at a river discharge rate of 48 m$^3$/s.
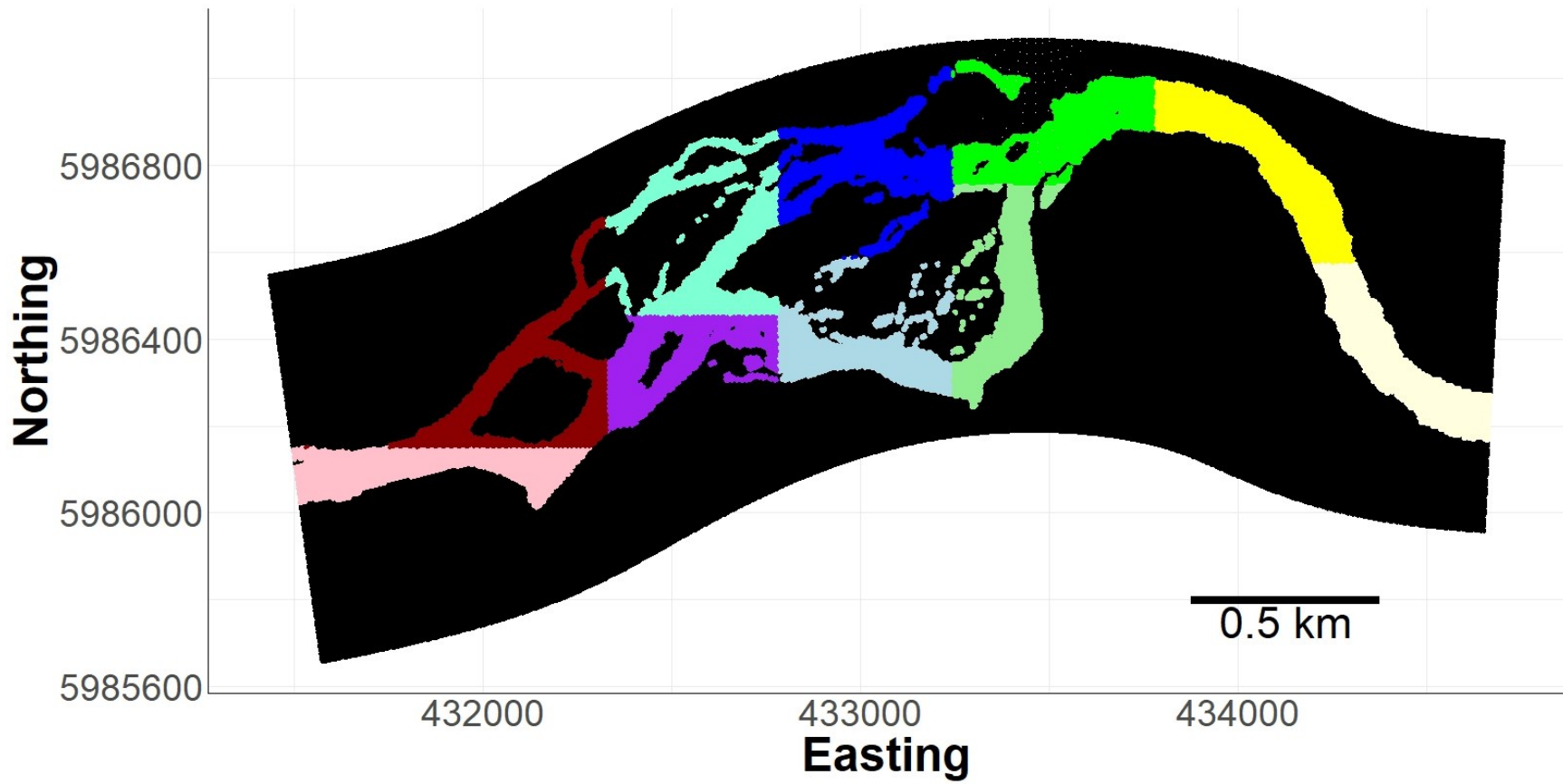
**Figure 6**    The ten different sub-areas for the site-specific egg mat array.
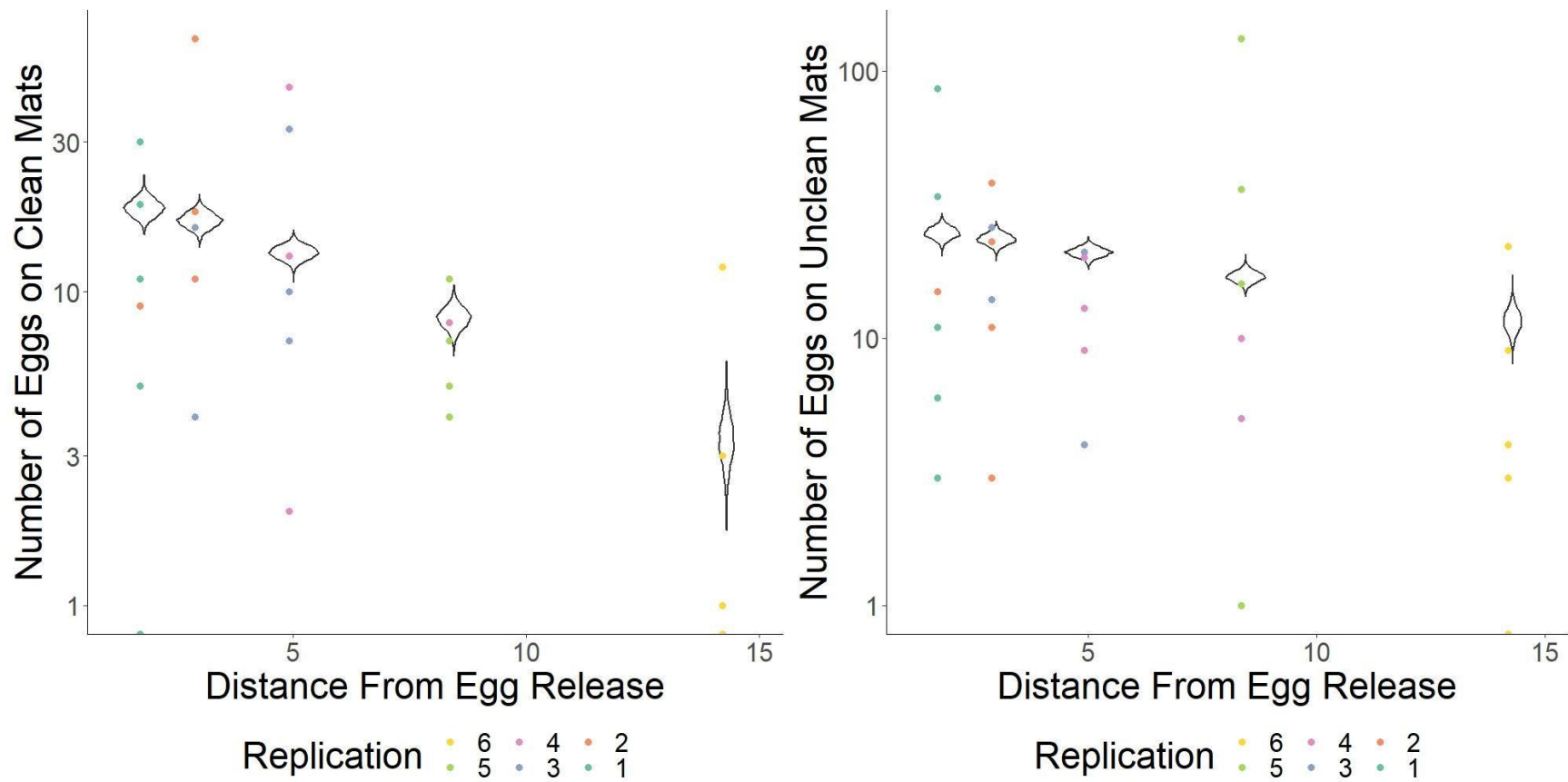
**Figure 7**    Posterior predictions (violin plots) compared to data (points). Data points are coloured according to the six release replications. Number of eggs released for each replication was roughly 1000 and calculated volumetrically.
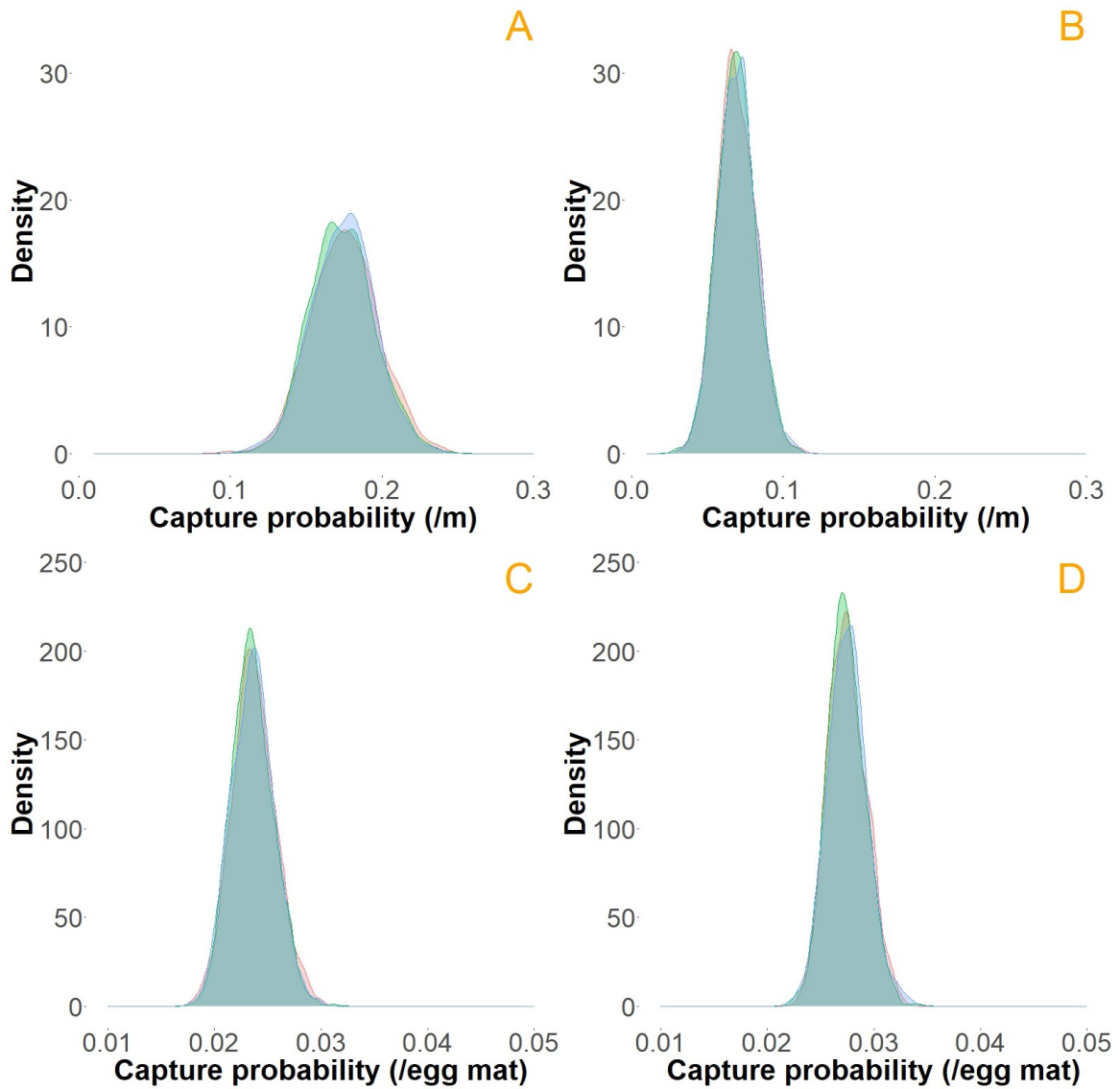
**Figure 8**    Density plots displaying the posterior density of capture probability of clean (A) and unclean (B) substrates, as well as egg mats in clean (C) and unclean (D) environments. Different colored distributions represent the posteriors for each MCMC chain.
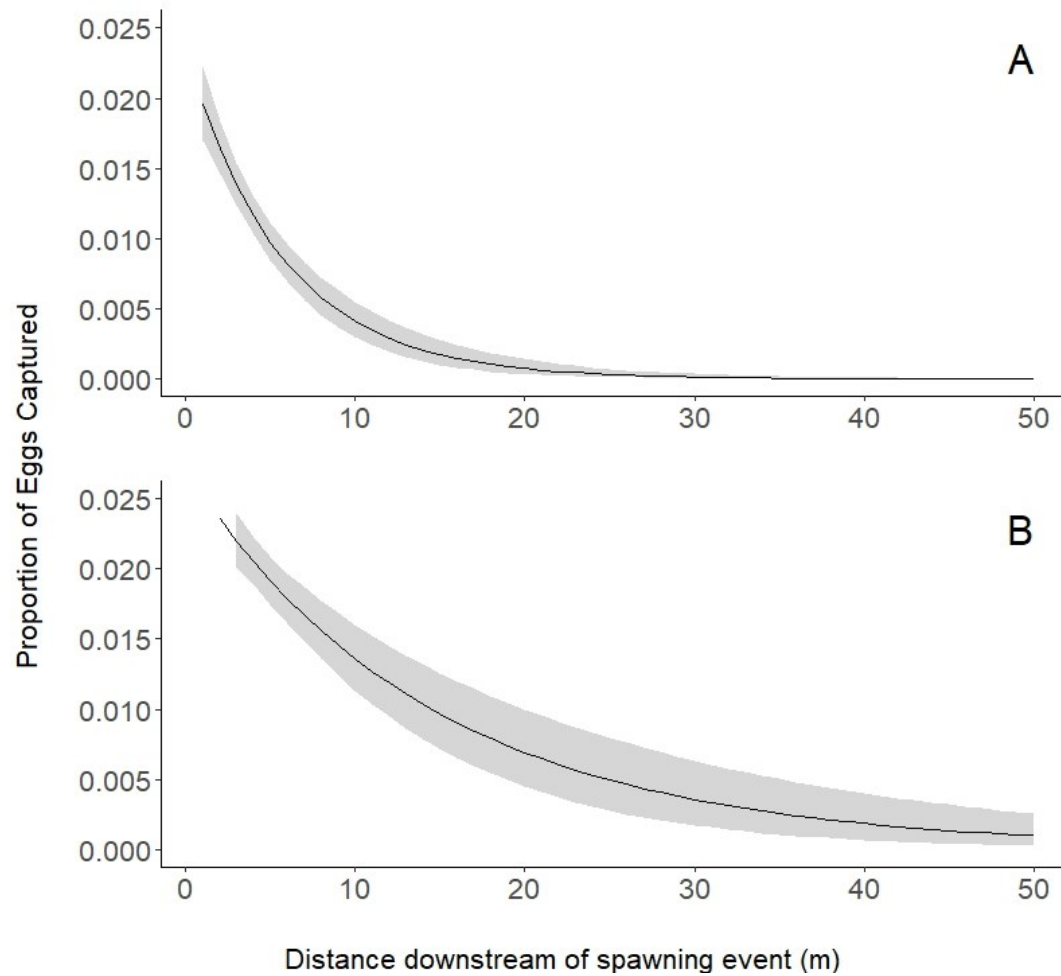
**Figure 9** Predicted proportion of embryos captured on an egg mat downstream of a spawning event in cleaned (A) and uncleaned (B) habitat conditions. Embryo release is assumed to occur 0.3 m above the substrate at a water velocity of 0.86 m/s. Note that embryos are considered adhesive from the moment they are spawned in these predictions (as they had been fertilized for 1:15 minutes prior to release), which may not be the case under natural circumstances.
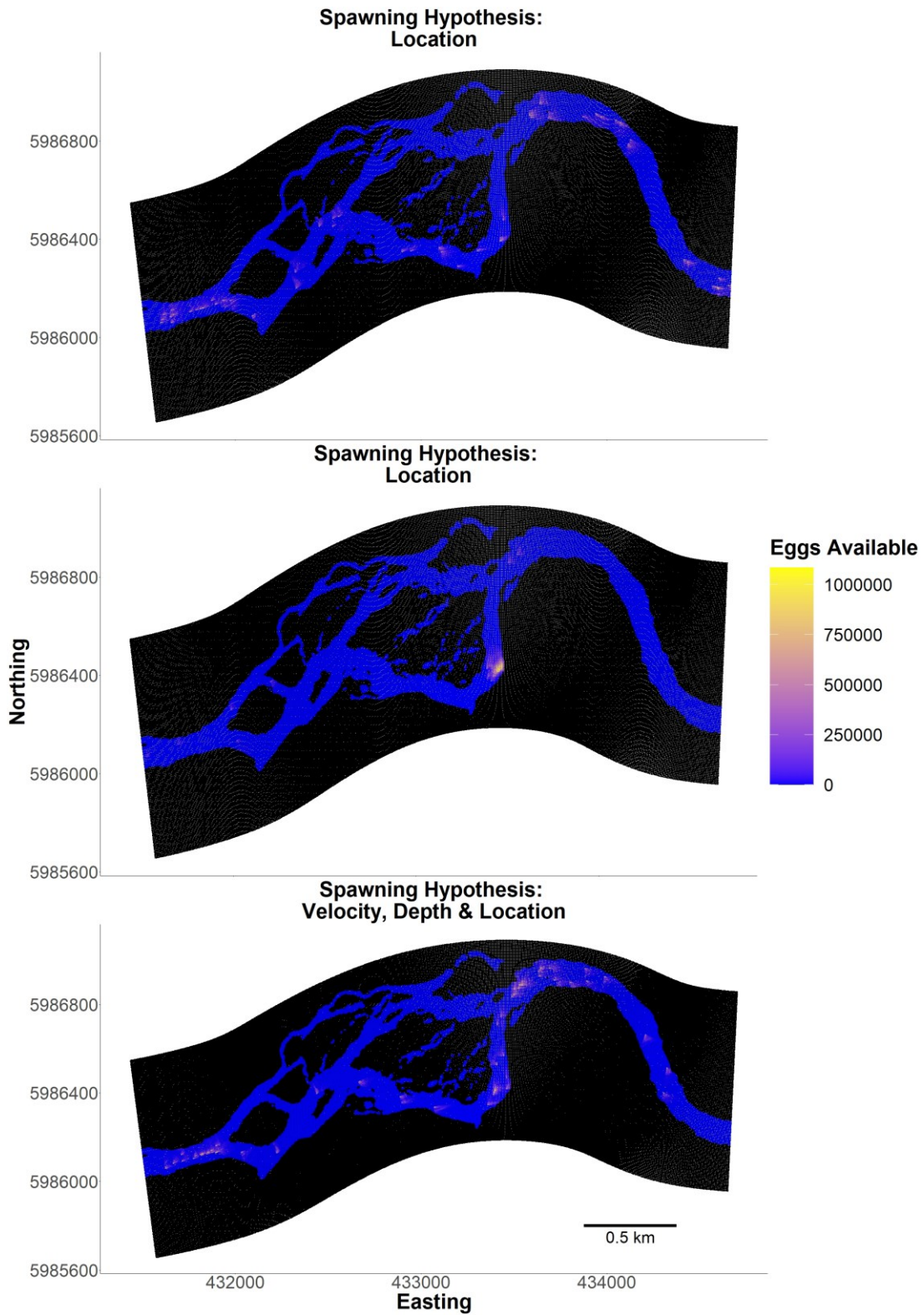
**Figure 10**    An example of the spatial distribution of egg settlement in a single year given each strategy at a river discharge rate of 48 m3/s. 250,000 eggs were simulated to have spawned at each of the 50 spawning locations determined based on the indicated spawning hypothesis.

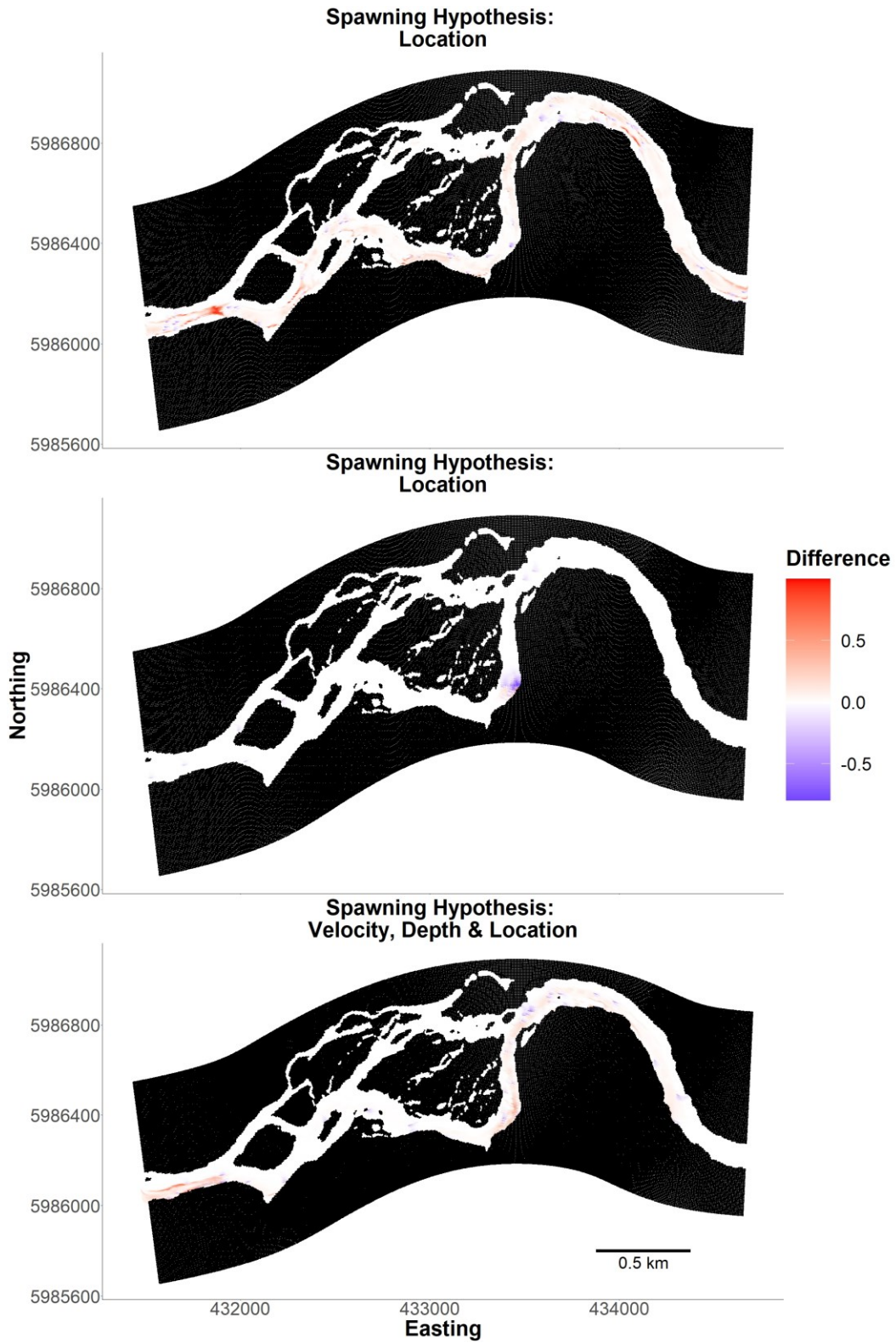**Figure 11**    Mis-match between the predicted and simulated probability of spawning for each spawning hypothesis at a river discharge of 48m³/s. Red instance indicates a higher predicted probability of spawning than what was simulated.
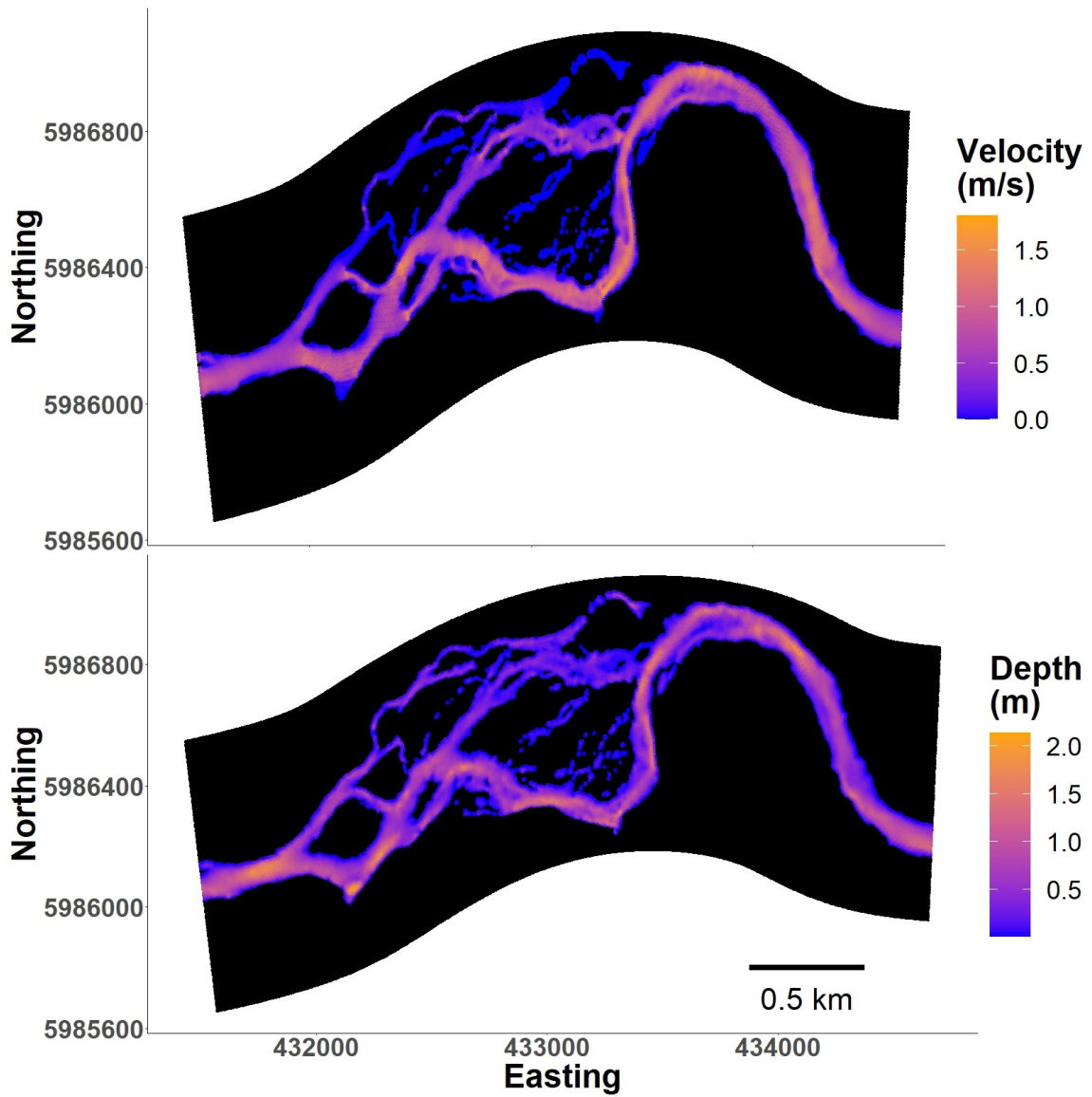
**Figure 12**   The velocity (m/s) and depth (m) of the river at a river discharge of 48 m$^3$/s.

# Appendix.

## Supplementary Figures
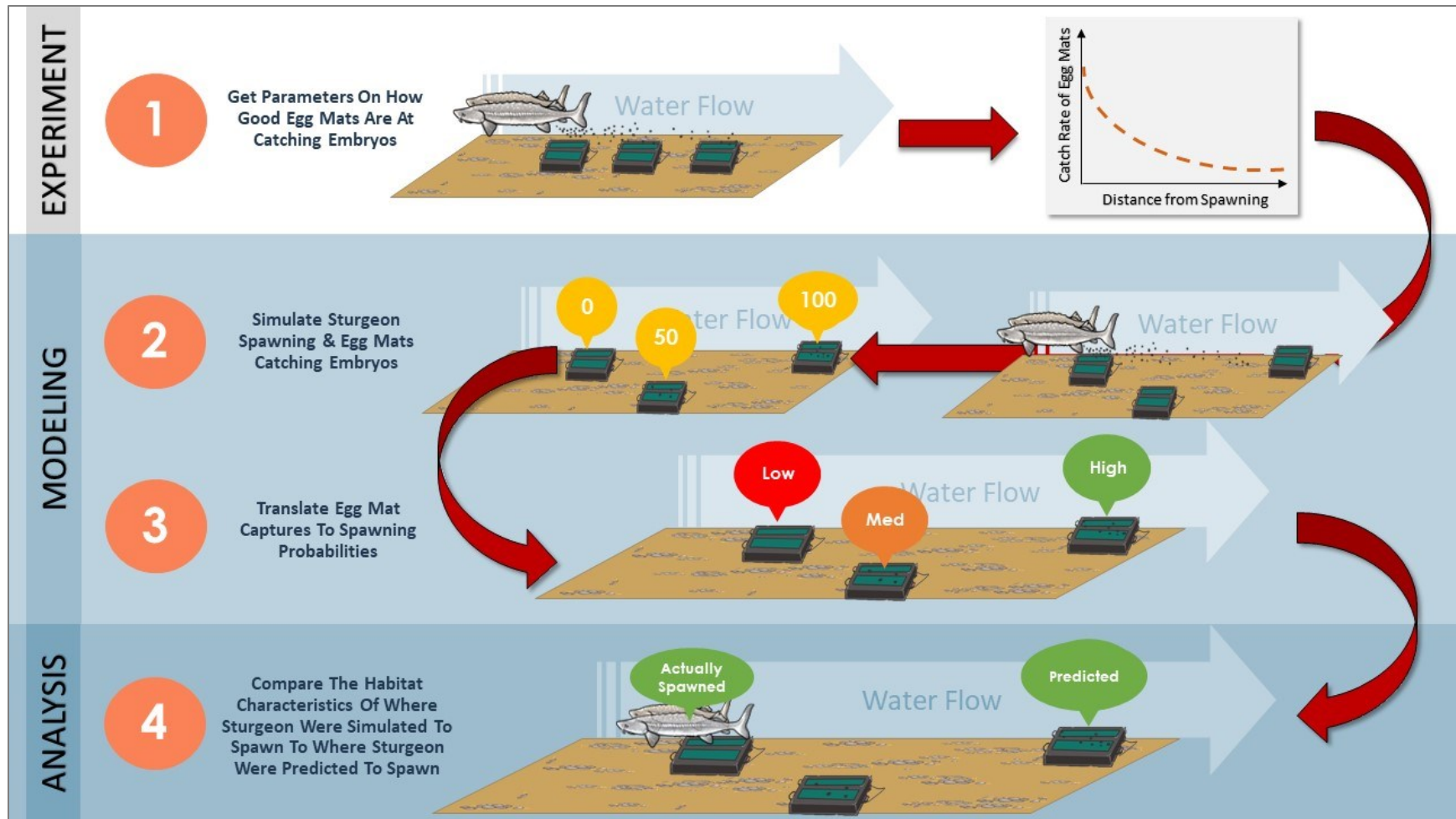
**Figure A.1**     Schematic displaying the process of this study, the methedologies used, and how they relate to each step of the process.
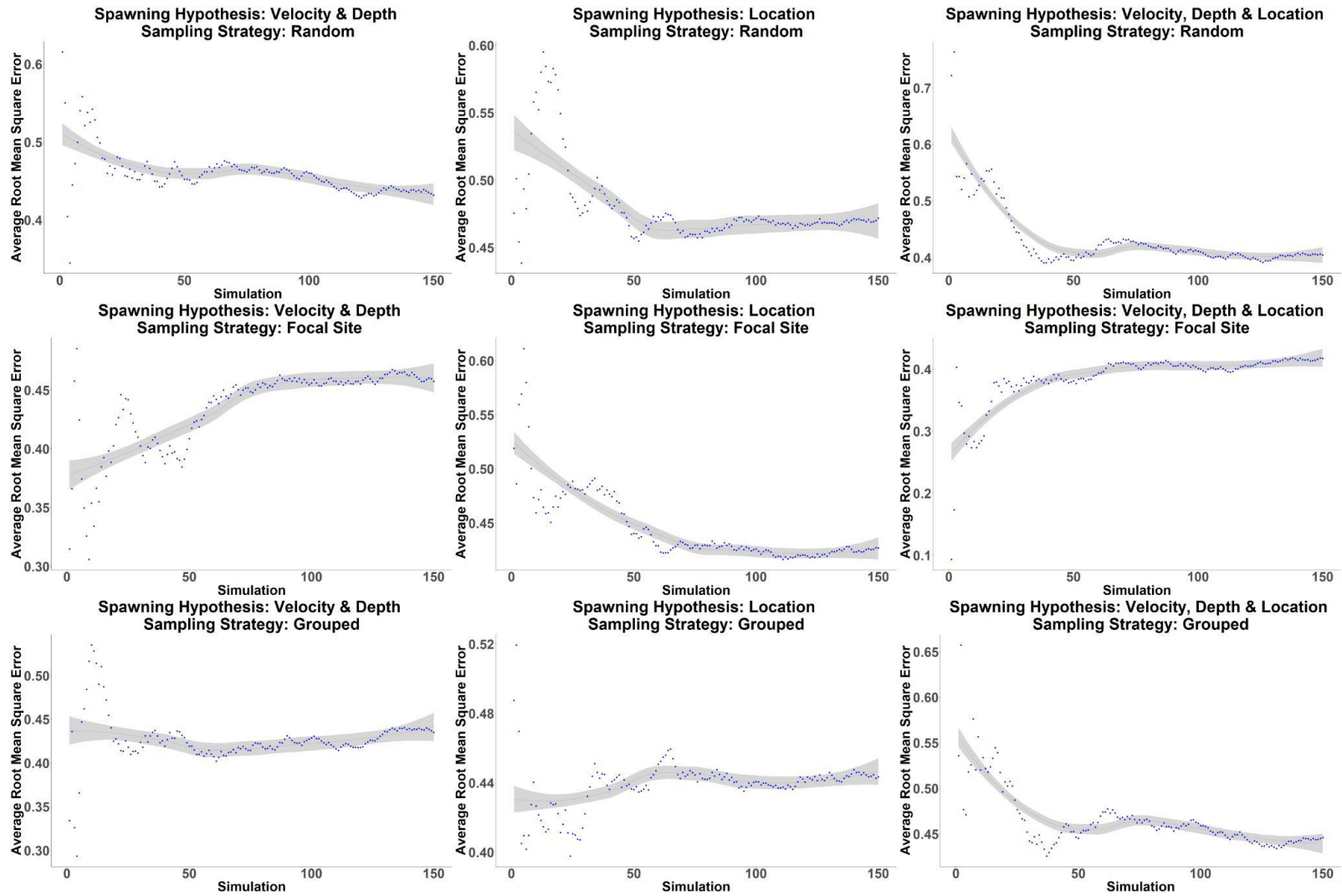
**Figure A.2**    Average Root Mean Square Error (RMSE) value between simulated and estimated spawning probabilities for each of 150 iterations the predictor variables of depth, velocity and location.

**Table A.1**  Model comparison displaying AIC outputs for the 150 simulation-estimation iterations, when data was generated using location as the environmental variable driving spawning site selection.

| Estimation model (GAM) | AIC median | 90th percentile AIC range | Δ AIC median | 90th percentile Δ AIC range | AIC weight median | 90th percentile AIC weight range |
|---|---|---|---|---|---|---|
| | | | Environmental variables influencing sturgeon spawning site selection: location | | | |
| | | | Random egg mat sampling strategy | | | |
| Velocity & depth | 152845.4 | 44520.3 – 387064.9 | 143140.8 | 37177.0 – 339188.6 | 0.0 | 0.0 – 0.0 |
| Location | 32709.9 | 8628.5 – 78328.4 | 17586.1 | 3443.1 – 40929.2 | 0.0 | 0.0 – 0.0 |
| Velocity, depth & location | 12296.6 | 2692.4 – 44507.3 | 0.0 | 0.0 – 0.0 | 1.0 | 1.0 – 1.0 |
| | | | Site-specific egg mat sampling strategy | | | |
| Velocity & depth | 94295.6 | 2820.2 – 478951.6 | 87999.0 | 1565.3 – 445267.8 | 0.0 | 0.0 – 0.0 |
| Location | 20273.0 | 961.6 – 103636.3 | 9700.8 | 334.6 – 52096.4 | 0.0 | 0.0 – 0.0 |
| Velocity, depth & location | 7645.5 | 171.3 – 56347.0 | 0.0 | 0.0 – 0.0 | 1.0 | 1.0 – 1.0 |
| | | | Random groupings egg mat sampling strategy | | | |
| Velocity & depth | 38384.1 | 2819.1 – 170387.3 | 36555.0 | 2108.9 – 165540.7 | 0.0 | 0.0 – 0.0 |
| Location | 5805.7 | 353.6 – 25594.3 | 3852.1 | 231.3 – 18306.2 | 0.0 | 0.0 – 0.0 |
| Velocity, depth & location | 917.7 | 75.8 – 8129.6 | 0.0 | 0.0 – 0.0 | 1.0 | 1.0 – 1.0 |

**Table A.2**    Model comparison displaying AIC outputs for the 150 simulation-estimation iterations, when data was generated using velocity and depth as the environmental variables driving spawning site selection.

| Estimation model (GAM) | AIC median | 90th percentile AIC range | Δ AIC median | 90th percentile Δ AIC range | AIC weight median | 90th percentile AIC weight range |
|---|---|---|---|---|---|---|
| Environmental variables influencing sturgeon spawning site selection: velocity & depth | | | | | | |
| Random egg mat sampling strategy | | | | | | |
| Velocity & depth | 203245.6 | 134318.9 – 274145.8 | 3912.4 | 0.0 – 22116.1 | 0.0 | 0.0 – 1.0 |
| Location | 234030.7 | 143469.2 – 323590.8 | 36661.6 | 16114.0 – 72636.5 | 0.0 | 0.0 – 0.0 |
| Velocity, depth & location | 199715.1 | 124908.2 – 285258.0 | 0.0 | 0.0 – 20589.2 | 1.0 | 0.0 – 1.0 |
| Site-specific egg mat sampling strategy | | | | | | |
| Velocity & depth | 196498.4 | 117116.8 – 273363.4 | 9236.0 | 0.0 – 34261.6 | 0.0 | 0.0 – 1.0 |
| Location | 216518.2 | 128945.3 – 316681.8 | 29887.3 | 12324.2 – 66023.6 | 0.0 | 0.0 – 0.0 |
| Velocity, depth & location | 185095.0 | 113086.2 – 262558.4 | 0.0 | 0.0 – 13868.7 | 1.0 | 0.0 – 1.0 |
| Random groupings egg mat sampling strategy | | | | | | |
| Velocity & depth | 85993.3 | 48017.1 – 27545.5 | 5436.8 | 0.0 – 27545.5 | 0.0 | 0.0 – 1.0 |
| Location | 99751.3 | 53470.1 – 168856.7 | 20231.2 | 6818.6 – 41561.3 | 0.0 | 0.0 – 0.0 |
| Velocity, depth & location | 78600.0 | 45400.3 – 135705.7 | 0.0 | 0.0 – 6236.8 | 1.0 | 0.0 – 1.0 |

**Table A.3** Model comparison displaying AIC outputs for the 150 simulation-estimation iterations, when data was generated using velocity, depth and location as the environmental variables driving spawning site selection.

| Estimation model (GAM) | AIC median | 90th percentile AIC range | Δ AIC median | 90th percentile Δ AIC range | AIC weight median | 90th percentile AIC weight range |
|---|---|---|---|---|---|---|
| Environmental variables influencing sturgeon spawning site selection: velocity, depth & location | | | | | | |
| Random egg mat sampling strategy | | | | | | |
| Velocity & depth | 216301.9 | 136535.7 – 300243.8 | 62954.6 | 28760.1 – 100134.1 | 0.0 | 0.0 – 0.0 |
| Location | 178709.1 | 116764.6 – 274537.5 | 31876.4 | 15726.0 – 54891.1 | 0.0 | 0.0 – 0.0 |
| Velocity, depth & location | 144466.3 | 98278.2 – 231140.5 | 0.0 | 0.0 – 0.0 | 1.0 | 1.0 – 1.0 |
| Site-specific egg mat sampling strategy | | | | | | |
| Velocity & depth | 186367.1 | 107038.2 – 284040.7 | 61129.0 | 24914.1 – 113684.8 | 0.0 | 0.0 – 0.0 |
| Location | 154955.8 | 80562.0 – 259146.7 | 27297.6 | 8386.1 – 66859.4 | 0.0 | 0.0 – 0.0 |
| Velocity, depth & location | 122901.5 | 54224.3 – 200734.3 | 0.00 | 0.0 – 0.0 | 1.0 | 1.0 – 1.0 |
| Random groupings egg mat sampling strategy | | | | | | |
| Velocity & depth | 92174.8 | 43730.3 – 161733.1 | 33406.5 | 12953.5 – 63800.7 | 0.0 | 0.0 – 0.0 |
| Location | 76400.4 | 35911.2 – 133133.2 | 18836.0 | 6258.9 – 41685.4 | 0.0 | 0.0 – 0.0 |
| Velocity, depth & location | 53240.9 | 25297.7 – 103556.3 | 0.0 | 0.0 – 0.0 | 1.0 | 1.0 – 1.0 |