Insights from an individual based model of a fish population on a large regulated river

Article *in* Environmental Biology of Fishes · August 2019

DOI: 10.1007/s10641-019-00891-6

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Environ Biol Fish
https://doi.org/10.1007/s10641-019-00891-6

Insights from an individual based model of a fish population on a large regulated river

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Received: 11 June 2018 / Accepted: 13 June 2019

Abstract On regulated rivers, managers must understand how drivers they can influence interact with the system to affect the health of resident fish populations. One potential way to gain insight into how these drivers interact or act in insolation is with individual based models (IBM), which can take numerous environmental drivers as inputs and mechanistically simulate their effects on the individuals in the system. This paper uses inSALMO, a spatially explicit IBM for salmon freshwater life stages, to examine how eight different drivers affect nine response variables for winter run Chinook salmon on the Sacramento River, CA. This paper examines the effects spawner numbers, spawner timing, water temperature, flow rate, turbidity, habitat cover, gravel area, and food concentration on superimposition, temperature induced egg mortality, predation, stranding, poor condition mortality, age at out-migration, length at out-migration, number of out-migrants, and juvenile size distribution. Notable results included: flow's lack of effect on juvenile stranding and small effect on final out-migrant count, the degree to which flow affects superimposition risk, temperature having the largest effect on final juvenile out-migrant count, the interaction between predation and temperature induced egg mortality which produces a constantly decreasing out-migration count with temperature, and the level at which gravel additions would not have added benefits for superimposition mortality. While this method uses simulations, and thus will not have perfectly fidelity to the system, it is a cost-effective and quick method for gaining a mechanistically derived understanding of the complex relationships between numerous drivers and response variables.

Keywords Chinook salmon · IBM · Modeling · River · Behavior · Physiology

Introduction

Many anadromous fish populations currently spawn in regulated rivers below dams (Murchie et al. 2008). On these riverine systems, there are many ecological drivers that can interact in complex ways to affect resident fish life histories (Schlosser 2017). Humans often have limited control over several of these ecological drivers (Krause et al. 2005), and, when managing these drivers, often consider the health of resident fish populations. The complex interactions between these drivers makes analysis of their effects on fish populations and their management difficult. As the number of drivers is often large, it is impractical to conduct field experiments

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10641-019-00891-6) contains supplementary material, which is available to authorized users.

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which cover the range of possible combinations, or control field conditions adequately to isolate a single driver.

Individual based models (IBMs) are one potential method for learning more about the relationships between drivers and fish populations. As models that simulate autonomous individuals and their interactions with a system, IBMs can incorporate numerous drivers and mechanistically model how they affect an individual. IBMs also model the interactions between individuals and can analyze the system in aggregate to understand whole system properties such as density dependence. This approach allows modelers to analyze individual driver effects on single response variables, compare effect of drivers acting in isolation or in unison, find driver thresholds which change system behavior, and isolate effects on different age or size classes of fish. These features make IBMs useful tools for examining fish population dynamics in large regulated rivers, such as the Sacramento River in California's Central Valley.

Here, I use a previously validated IBM (inSALMO) (Railsback et al. 2013; Dudley 2018) of juvenile endangered Sacramento River winter run Chinook (SRWRC) salmon (*Oncorhynchus tshawytscha*) to examine the population effects of several ecological drivers. In several ways the Sacramento River is representative of many North American rivers. It is dammed, similar to 43 of North America's 74 large rivers (mean annual flow over 350 m^3/s) (Dynesius and Nilsson 1994) and heavily used for urban and agricultural water supply. Similar to 56,000 km^2 of watershed in OR, WA, and CA, concerns about endangered salmonids greatly impact the management of the Sacramento River (NOAA 2010).

I used inSALMO to examine how changing both a single driver and changing correlated drivers in unison impact SRWRC population dynamics. The set of drivers included variables known to impact salmon population dynamics: spawner numbers, spawner arrival window length (timing), water temperature, flow rate, turbidity, predation and velocity cover, gravel area, and drift food concentration. The SRWRC response variables include superimposition, temperature induced egg mortality, predation, stranding (fish being trapped without access to water), poor condition mortality, age at out-migration (age at which juveniles leave the model domain), length at out-migration, number of out-migrants (number of juveniles that leave the model domain alive), and size distribution. I analyzed the effects of changing the correlated key drivers of temperature, turbidity and flow together. I found that the simulations responded to many drivers in expected ways, matching experimental observations, and responded to some in unexpected or non-obvious ways. When the correlated drivers of temperature, turbidity, and flow vary together, which of the three has the dominant effect varies across response variables. The other two correlated drivers frequently influence the fine scale behavior of the response variable or change the magnitude of the main driver's effect. Notable results include: a large number of density dependent effects, no effect of flow on juvenile stranding, a small effect of flow on final out-migrant count, the extent of the effect of flow on superimposition risk, the dominant effect of temperature on final juvenile out-migrant count, the peak in the relation between predation risk and temperature, the way predation and temperature induced egg mortality interact to produce a constantly decreasing out-migration count with temperature, and the threshold at which gravel additions would not have added benefits for superimposition mortality. Overall, this IBM method aids in the understanding of fish population dynamics on regulated rivers and offers guidance on what future field experiments and habitat restoration measures may be most informative for managers.

Methods

The details of the modeling software inSALMO are described in Railsback et al. (2013), in the "overview, design concepts, and details" format (ODD). In brief, inSALMO models the freshwater life stages of salmon on a daily time step. There are three biological entities for salmon in the model [adults, redds (a group of eggs), and juveniles (fry/smolts)]. Habitat is represented in two spatial entities in the model (reaches and cells). Reaches have a single daily temperature, daily flow, daily turbidity, and constant food availability. Each reach contains multiple cells. Each cell has its own daily velocity, daily depth, constant percent cover, and constant percent gravel.

After spawning in a cell, adults guard their redd until they die. The eggs in the redd develop at a temperature dependent rate and can experience mortality from high/low temperature, scour, dewatering, or superimposition (a female salmon establishing a redd on top of an existing redd). After juveniles emerge they begin to feed on drift food and grow. Turbidity, water velocity, fish size, and duration of daylight all affect feeding duration and efficiency. The juveniles suffer mortality from predation, stranding, poor body condition, and water temperature. Turbidity, cover, water depth and temperature, duration of daylight, and juvenile size all affect the risk of predation. Eventually, growth to an adequate size, or lack of good habitat will cause them to migrate to downstream reaches and finally out of the modeled system.

inSALMO requires several data sources and support programs to produce four types of inputs (Fig. 1). The model domain is a 96 km portion of the Sacramento River from Keswick Dam to just passed Red Bluff Diversion Dam (RBDD) divided into six approximately equal length reaches (Fig. 2). In these simulations, the inSALMO grid size is 20 m^2 which is small enough to allow small juveniles to explore nearby cells but large enough to provide adequate food for large juveniles.

Converting reach level flow into cell level depth and velocity required river bathymetry and hydrologic modeling. This inSALMO deployment uses a HEC-RAS 5.0.3 (Hydrologic Engineering Center 2016) hydrologic model with a structured simulation grid of 625,335 cells with 9.15 m^2 grid size overlaid on a 3.05 m resolution raster. This raster is made from a triangular irregular network (TIN) file made during CDWR and the Army Corps' Hydrologic Engineering Center's *Sacramento and San Joaquin River Basins Comprehensive Study* in 2001 (U.S. Army Corps of Engineers 2001). The TIN riverbed morphology is interpolating between cross sectional surveys, with cross section spacing between 1.3 and 0.16 km depending on local morphology.

The model used a Manning's N from a previously validated CDWR 1D HEC-RAS model and used that previous model's Anderson Cottonwood Irrigation

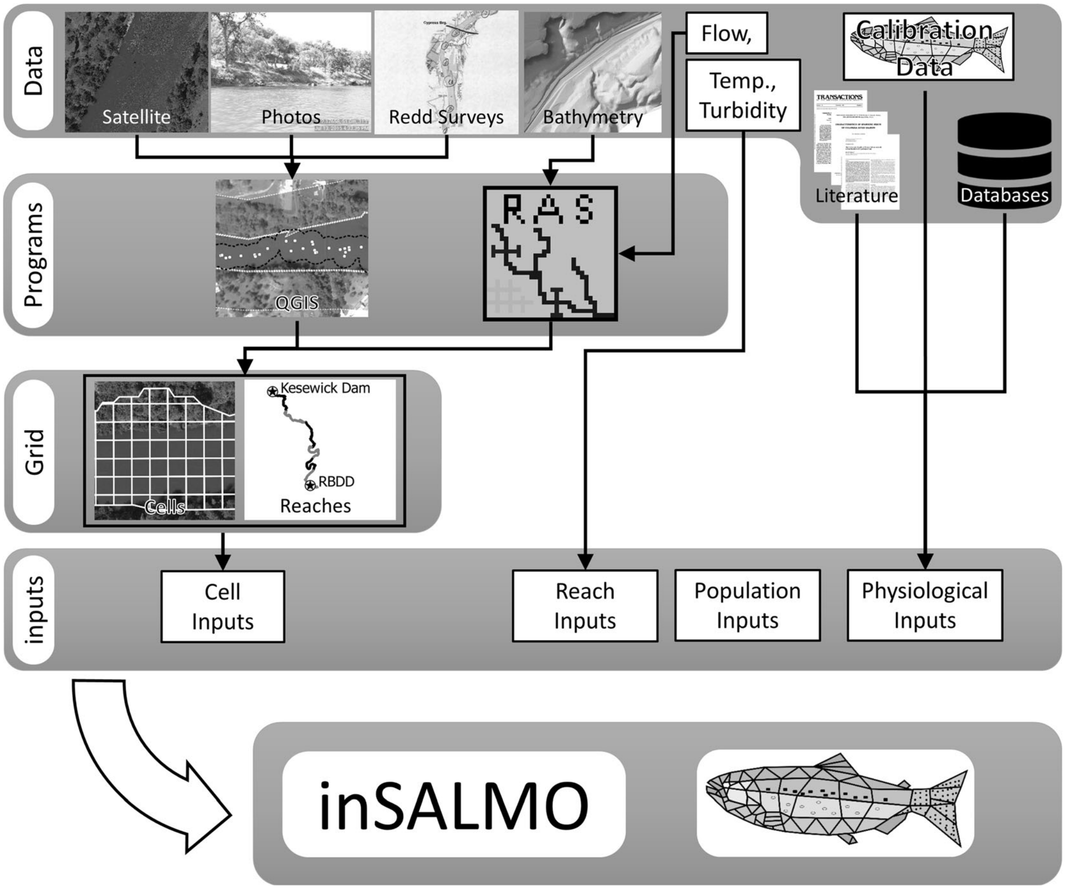


Fig. 1 A flow diagram of the model data inputs and components. The top cell shows the data sources, the second cell shows the programs that transform the data from the sources into inSALMO inputs, the third cell shows the grid which interpolates the data into the correct spatial resolution and extent for inSALMO, and the fourth cell lists the four classes of inputs inSALMO takes

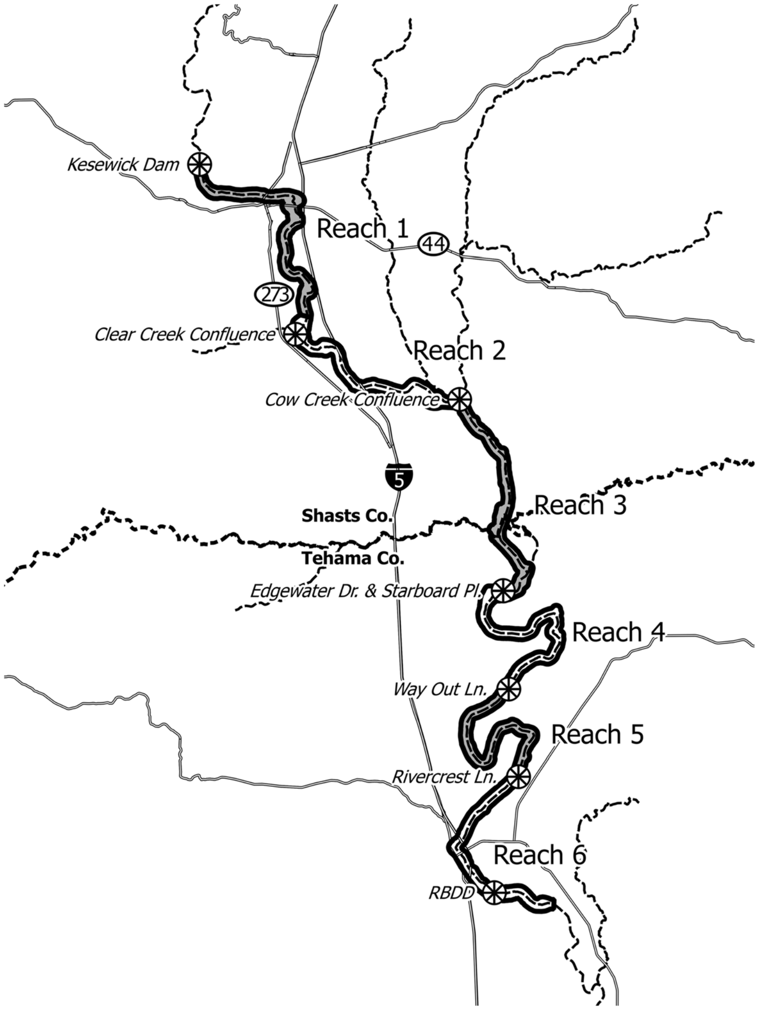


Fig. 2 All six reaches of the inSALMO run highlighted on a map. Location labels divide up the six reaches. All the spawning occurs in reach 1 with the majority occurring in the upper half

District Diversion Dam profile. I ran scenarios with flows from 56.6–453.1 m^3/s incrementing by 28.3 m^3/s and then from 566.3–22,653 m^3/s incrementing by 566.3 m^3/s. Each simulation produced both a velocity raster with 9.15 m^2 resolution and a depth raster with 3.05 m^2 resolution (Appendix S1: Fig. S2). Those rasters averaged over the inSALMO 20 m^2 grid are the first of two cell input files (Fig. 1) (cell velocity and depth).

I used a combination of satellite imagery (Google 2016) and ground based photos to set cover from predation (distance to cover) and cover from flow (percent cover). Polygons in a shapefile represented areas with consistent levels of cover. Levels of cover were 10%, 50%, or 100% cover (main channel, over bank, and noticeable cover respectively) (Appendix S1: Fig. S3). The base cover shape file had 80 km^2 of cover, which was about 65% of the model domain. The distance to cover equaled 16 m (the average distance between an internal point and a specific corner of a 20 m square) multiplied by 1 minus the fraction of cover (Eq. 1).

$$\text{Distance to Cover (m)} = 16\,(1-\text{Fraction Cover}) \quad (1)$$

To determine the total spawning gravel present in the system, this model used a similar approach to past Sacramento River gravel assessments (Stillwater Sciences 2007). This approach used the locations of SRWRC redds from 1995 to 2013 surveys and assumed there was gravel for some buffer distance around each redd location. The selected buffer distance resulted in the amount of gravel in a 3.3 km section of the Sacramento River equaling the amount found in a detailed visual survey over the same section (North Stare

Resources 2012). The buffer distance was 36 m of gravel around every SRWRC redd resulted in a base gravel area of 1.1 km^2; however, as many of the buffers overlap significantly, not every redd contributes 36 m radius circle worth of gravel (Appendix S1: Fig. S4). Those three polygon layers averaged over the 20 m^2 inSALMO grid were the second set of cell input files (Fig. 1) (cell habitat quality).

Physiological and behavioral parameters came from literature and available databases (Appendix S1: Table S1). If available, the parameters were based on data for SRWRC. If no SRWRC data existed, then the parameter was based on data from California populations of Chinook, then data from Chinook in general, or finally data from salmonids in general. R version 3.2.2's (R Core Team 2015) base package function glm performed the necessary logistic or linear fitting (e.g. Appendix S1: Fig. S5). When there was insufficient data for statistical fitting, I fitted the data by eye (e.g. Appendix S1: Fig. S6). There was insufficient data for statistical fitting for four parameters (max move distance, the effects of turbidity, size, and temperature on predation). For some physiological relationships with complex shapes (e.g. C_{max} vs. temperature) inSALMO uses a set of control points and linear interpolation to calculate values. I selected control points attempting to capture important aspects of the relationship (e.g. Appendix S1: Fig. S7). Dudley (2018) gives calibrated values for the four model parameters for which there was no data: the concentration of food (habDriftCon), the rate at which drift food regenerates (habDriftRegenDist) and the size at which juveniles perceive it to be safe to migrate downstream (fishOutmigrateSuccessL1 and fishOutmigrateSuccessL9).

For each experimental run, one driver changed from the following list: spawner number, spawner arrival window length, temperature, flow rate, turbidity, cover area, gravel area, and drift food concentration. When a driver was not the driver of interest, it had a base value of the 1996–2015 averages observed during the normal rearing time. The base values were: flow 254 m^3/s, turbidity 3.26 NTU, temperature 11.27 °C, drift food 2.2×10^{-9} g/cm^3, gravel area 1.1 km^2, cover area 80 km^2, number of spawners 5318 individuals, and arrival window length 81 days. There were also a "lower population" series of experiments with 1285 spawners in the system, based on the average of the 5 years with the lowest number of spawners from 1996 to 2015. The "lower population" set of experiments is designed to evaluate if response variables behave differently at a different population level. To ensure that values cover the observed range of values in the system, flow, temperature, and turbidity, ranges were larger than the ranges used in the calibration/validation of this model (Dudley 2018): water temperature (8 to 16 °C), flow (150 to 500 m^3/s), turbidity (0 to 30 NTU), drift feeding food density (1.0×10^{-10} to 1.4×10^{-8} g/cm^3), and the window over which spawners could enter the system (25 to 200 days). The number of total spawners ranged from 500 to 14,500 (All female to male ratios were 0.63, the average from 1996 to 2015). Input files for different levels of experimental gravel had either a reduced or increased fraction of gravel cover, in 0.2 increments, for each cell in the first reach (where the vast majority of the spawning occurs in reality and all the spawning occurs in the model). Cover input files had 100% cover buffers (of buffer distance 2 m to 16 m) around the base level 100% cover polygons.

For data from 1996 to 2015 on this system, the following equations are the best fit linear relationships between temperature, turbidity, and flow:

$$U = 27.2 - 1.65T \tag{2}$$

$$F = 902 - 51.6T \tag{3}$$

where U is turbidity in NTU, T is temperature in °C and F is flow in m^3/s. When changing all three (temperature, turbidity and flow) temperature ranged from 8 to 16 °C, thus flow ranged from 489.2 m^3/s at 8 °C to 76.4 m^3/s at 16 °C and turbidity ranged from 14.5 NTU at 8 °C to 1.3 NTU at 16 °C.

This work considers the following response variables which are either known sources of mortality or important indicators for managers: superimposition mortality, temperature caused egg mortality, predation, stranding, poor condition mortality, age at out-migration, length at out-migration, number of out-migrants, and out-migrant size distribution (how many juveniles are in each of three size classes). Superimposition mortality is the number of eggs dying due to superimposition divided by the total number of initially viable eggs. Predation/stranding risk is the number of juveniles predated/stranded each day of the simulation divided by the total number of fish alive that day. The yearly averages for these measures is the average of the daily values of these measures weighted by the number of juveniles alive each day. As mortality from poor condition is not an instantaneous event but develops over time, it is the number of poor condition mortalities from the whole simulation divided by the number of successfully emerged fry. For comparison purposes and to avoid having the large number of small juveniles swamp an important shift occurring with the larger juveniles, there are three size classes of out-migrants, small (under 5 cm), medium (5 to 8 cm), and large (over 8 cm). For each relation between a driver and response variable, I conducted a Spearman correlation tests with R version 3.2.2's base package function cor.test (R Core Team 2015). Bonferroni correction (Dunn 1961) corrected for multiple comparison.

Results

Adult stranding

Higher flows caused spawners to occupy deeper, higher velocity waters (Figs. 3 and 4), expend more energy on average (Fig. 5), and have a higher probability of dying from poor condition, which in turn reduced the probability of dying from stranding (Fig. 7). When considering temperature, turbidity, and flow together, flow had the dominate effect as both turbidity and temperature in isolation had no effect; however, there was an apparent interaction when all three were changed in unison as the effect size was larger than flow in isolation. All other relationships were not significantly correlated. There were similar relationships at the lower population level, but the relationships for flow had more scatter (Appendix S1: Fig. S8) Fig. 6.

Superimposition

There was a positive density dependent relationship with the fraction of eggs killed through superimposition and the number of spawners in the system (Fig. 7). There was a negative relationship between the length of the arrival window and the density of spawners in the system, which decreased the chances of superimposition; however, a stronger effect occurred where there were increasingly more new spawners in the system after the earlier ones had stopped guarding their redds, which increased the chances of superimposition. This mechanism only continued up to a certain arrival window length, after which new spawners entering the system were sufficiently spread out that eggs hatched before additional superimposition could occur. There was a positive relationship between flow rate and water velocities spawners experienced (Fig. 4), and energy loss rate of the spawners (Fig. 5), shortening their guarding time and resulting in more superimposition. There was a negative relationship between superimposition risk and the amount of spawning gravel, up to a threshold of about 1 km^2 total of gravel in reach 1, above which the effect was minimal. Considering temperature, turbidity and flow together, flow was the dominate driver in determining superimposition risk. There were similar relationships at the lower population level, without a significant correlation with flow, or gravel amount (Appendix S1: Fig. S9).

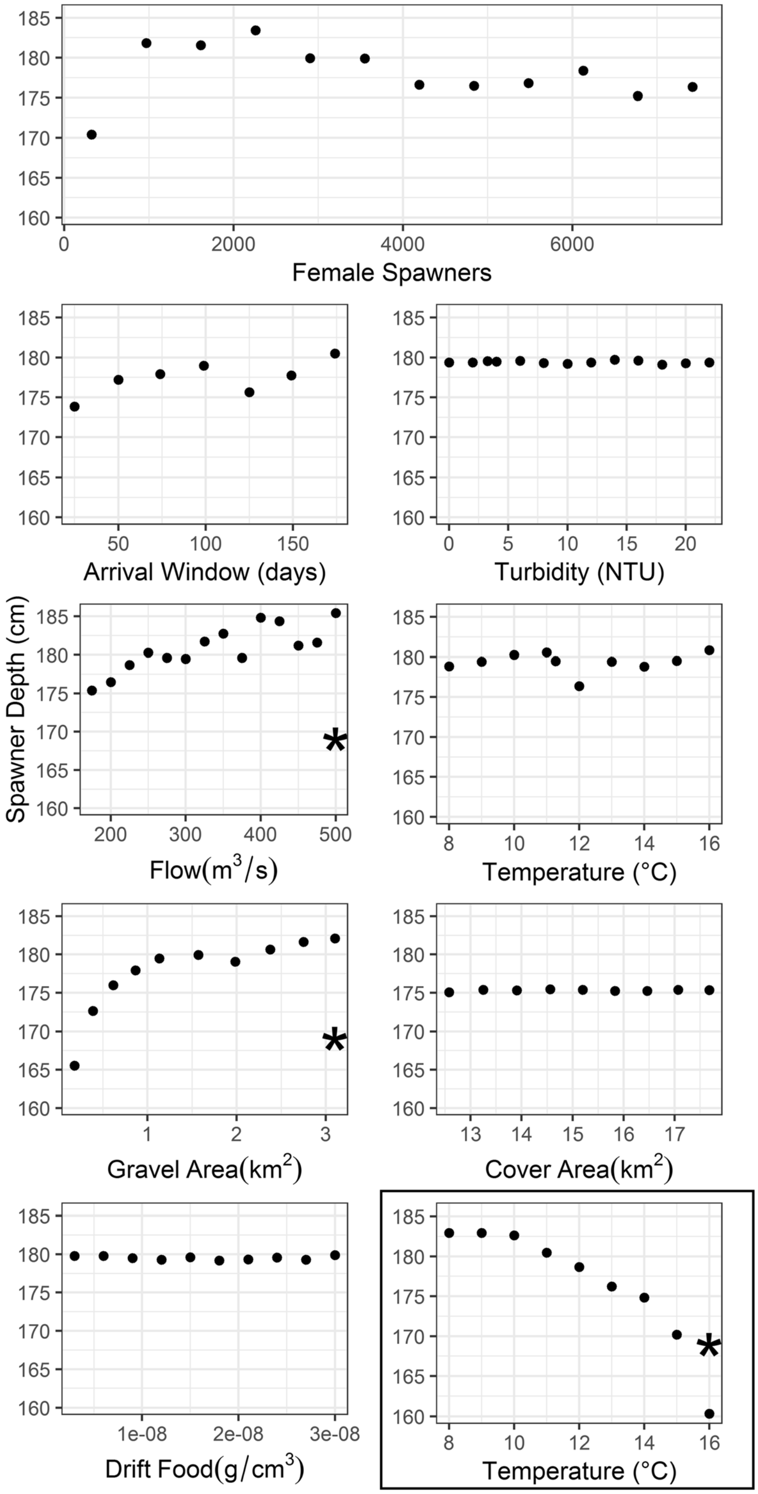
High temperature mortality

Temperature was the only variable that directly affected incubating eggs. Mortality approached 10% at 12 °C and increased rapidly thereafter (Fig. 8). There were no mortalities from scour or dewatering under the simulation conditions.

Predation

The per capita amount of habitat with close predation cover available was negatively related to the number of spawners (Fig. 9) and the risk of predation was positively related (Fig. 10) to the number of spawners. The predation risk stabilized above 5000 spawners, as each new juvenile spawned above that number immediately left the model domain (see *Age at Out-migration* section). Predation risk was negatively related to both the length of the spawner arrival window and turbidity, as the more turbid water provided juveniles with predation cover. Increased flow forced juveniles to swim in higher velocity waters and thus their net energy budgets decreased (Figs. 11 and 13). The lower net energy balance resulted in smaller juveniles which were more at risk of predation (see *Size Class Makeup* and *Out-migration Length* sections). Increased temperature directly increased predation risk on juveniles up to a threshold where higher temperature induced egg mortality reduced the density dependent effect of average distance to cover. Gravel area showed a density dependent artifact from superimposition (Fig. 7). Increasing cover reduced the ratio of juveniles to area with accessible cover, and thus reduced predation. When considering temperature, turbidity and flow together, temperature looked to be the leading driver of predation risk; however, there was not a significant correlation and instead the relationship appears to have a maximum. Similar relationships exist with the lower population (Appendix S1: Fig. S10) except drift food now had a significant correlation with predation risk by increasing juvenile size.

Fig. 3 The relationships between the set of environmental drivers and the average water depth spawners experience. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction



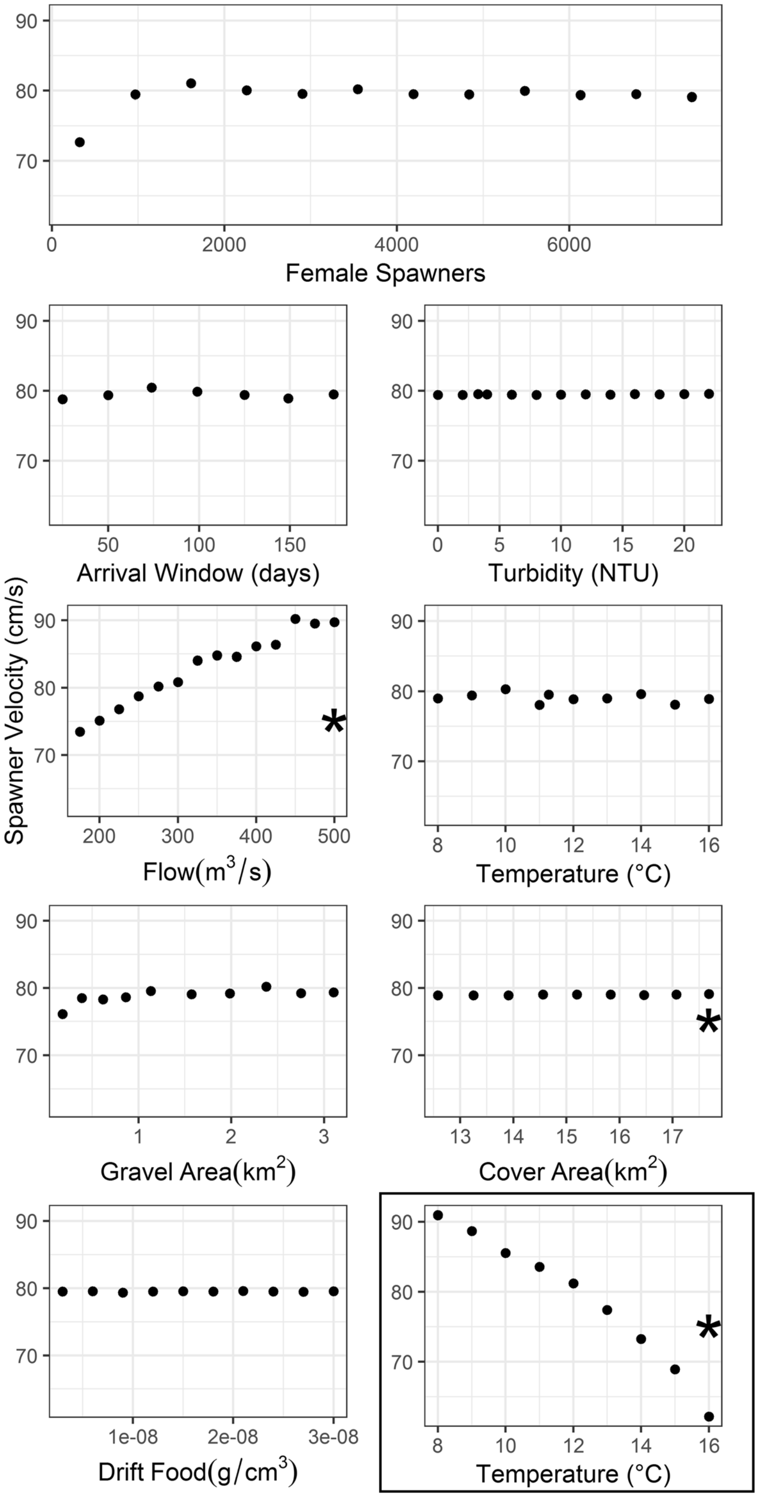


Fig. 4 The relationships between the set of environmental drivers and the average water velocity spawners experience. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

Fig. 5 The relationships between the set of environmental drivers and the average daily net energy use of spawners. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

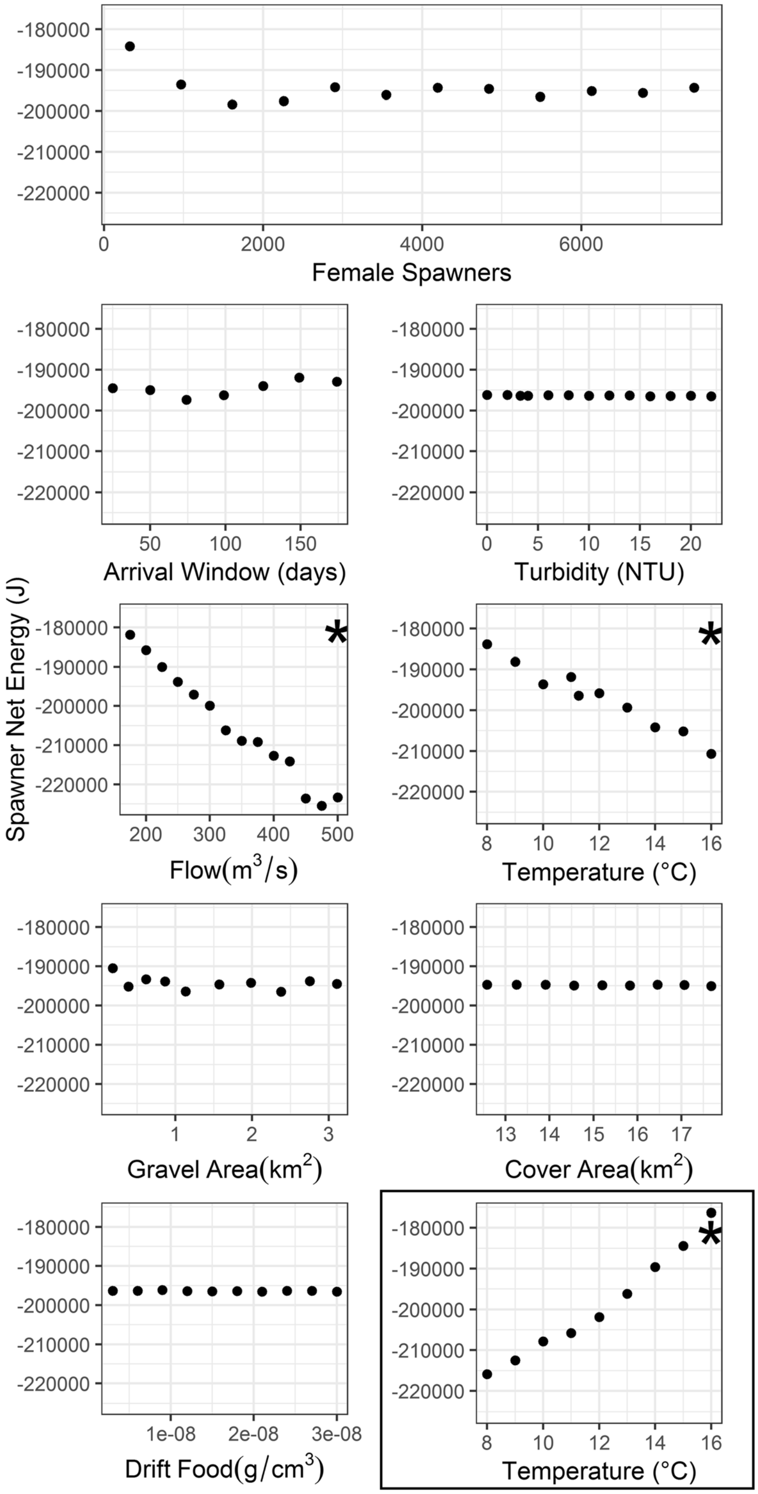


Fig. 6 The relationships between the set of environmental drivers and the amount of adult stranding per female. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

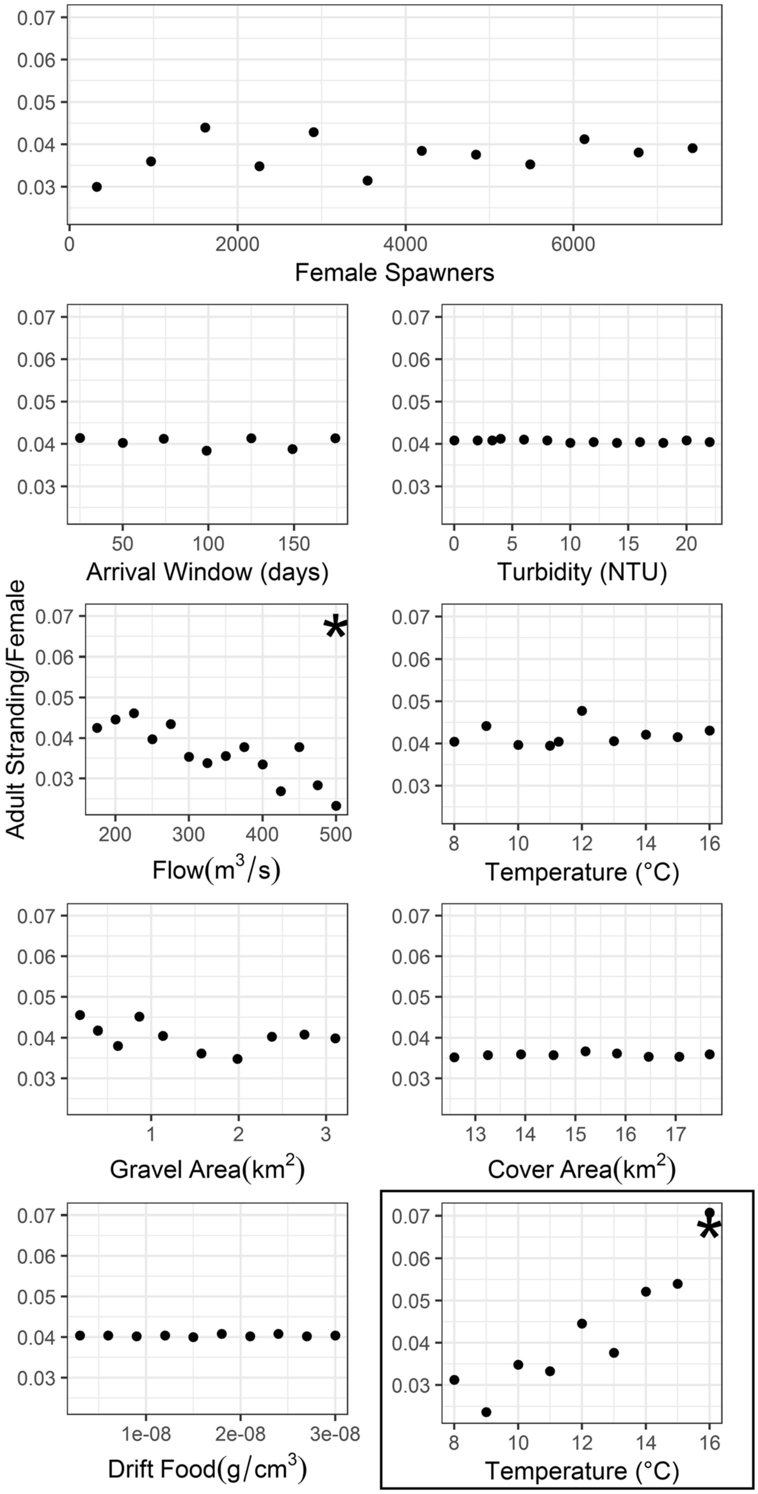
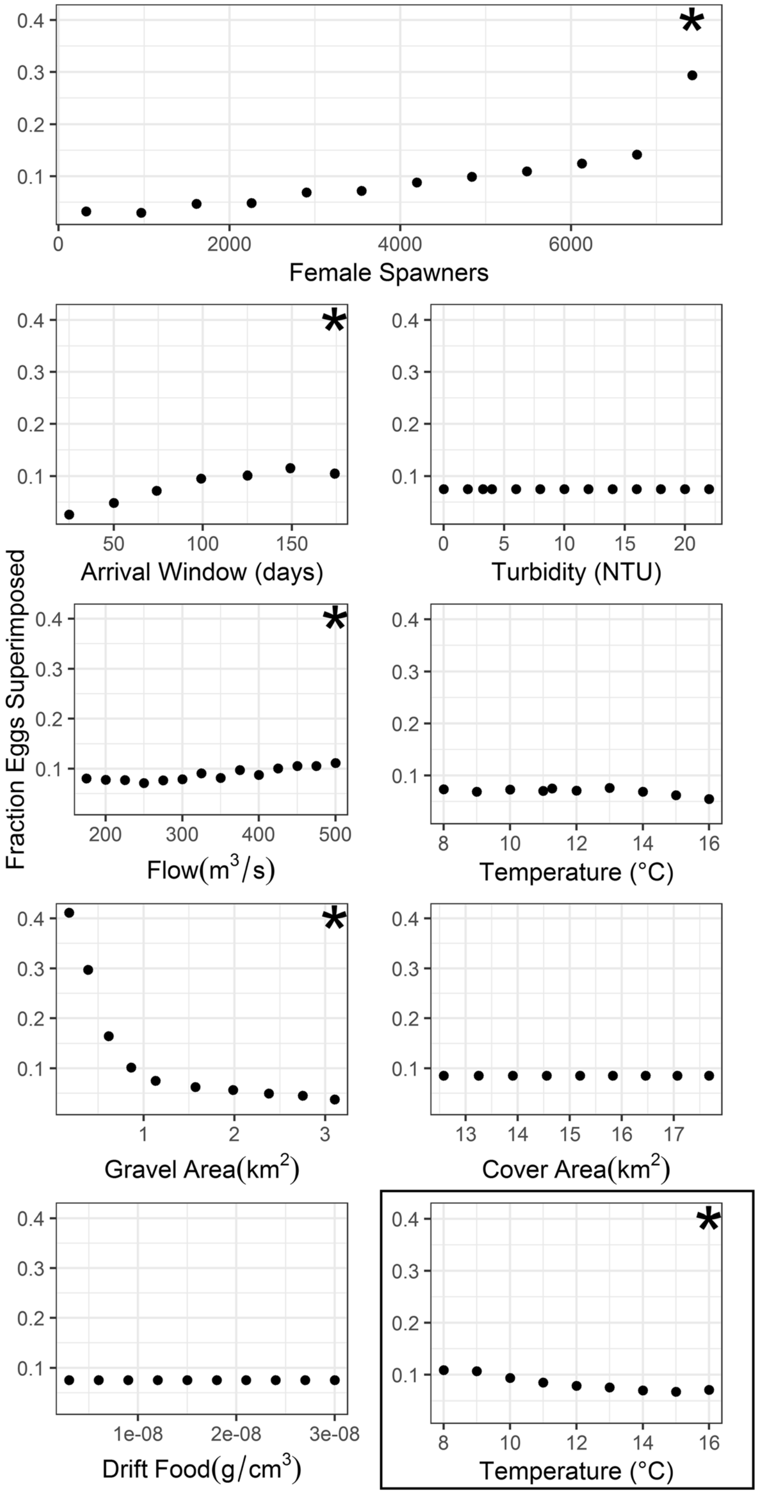


Fig. 7 The relationships between the set of environmental drivers and the fraction of eggs that die from superimposition. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction



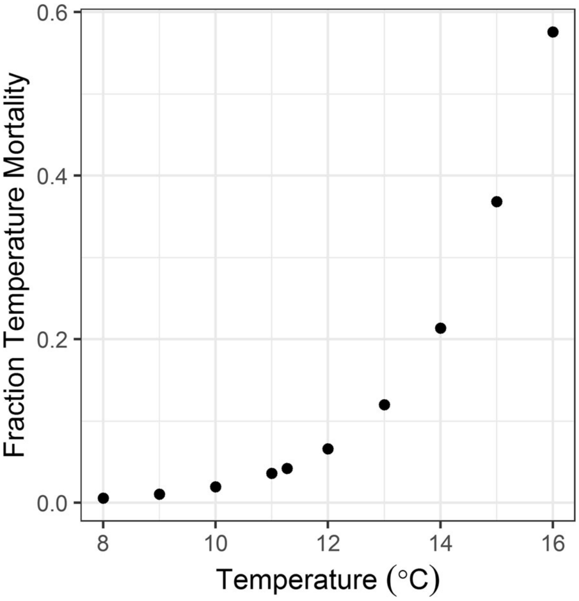


Fig. 8 The relationships between the temperature and the fraction of eggs exposure to high temperature kills

Poor condition mortality

Poor condition mortality had a lower impact on survival than predation. More spawners in the system produced density dependent phenomena which caused the juveniles to exit the system quicker and have less time to experience poor condition mortality (Fig. 13). Ability to detect prey decreased with turbidity, resulting in lower net energy intake (Fig. 12) and increased poor condition mortality. Increased flow forced juveniles to leave the system faster and so they had less time to suffer poor condition mortality. More cover lowered the ratio of juveniles to cover area, thus allowing juveniles to remain in lower velocity water safe from predation. These juveniles grew larger, which buttressed them against lower condition mortality; however, the high metabolic costs of these larger juveniles caused the average net energy intake for the year to decrease. More drift food decreased mortality from poor condition. When considering temperature, turbidity and flow together, the effect of turbidity was dominant on poor condition, but flow reduced the magnitude of this effect. At the lower population level, there were similar relationships but with less cover area required to reduce the poor condition mortality risk. (Appendix S1: Fig. S11) Fig. 13.

Stranding risk

In general, stranding risk was small compared to predation risk. There was a negative density dependent relation between spawners and stranding risk. More spawners allowed fewer juveniles to hide in shallow water (Fig. 14) thus decreasing stranding risk (Fig. 15). Increasing the arrival window had the same density dependent effect; the fraction of juveniles which were able to hide in shallow water increased. Increased turbidity decreased juvenile size (see *Out-Migrant Length* section) and the depth of the water they occupied. Smaller juveniles are less susceptible to stranding and, because the effect of change in size was larger than the effect of change in the depth of occupied water, the stranding risk decreased. Increasing temperature had little effect on stranding until high temperatures, where there were fewer juveniles due to higher egg mortality (Fig. 8), which allowed juveniles to hide in shallow water; thus, temperature was correlated with stranding risk. After passing a threshold, increased cover provided better sanctuary from predation than shallow water, allowing juveniles to move into deeper water while still avoiding predation and decreasing stranding risk. As temperature, turbidity, and flow varied, they acted together to increase stranding as temperature increased (flow and turbidity decreased) with greater magnitude than any of the three drivers produce in isolation. There were similar relationships in the lower population simulations, with the exception that temperature did not have a significant correlation (Appendix S1: Fig. S12).

Age at out-migration

An increased number of spawners or a shortened arrival window produced density dependent effects with other resources which caused juveniles to out migrate earlier; however, though statistically significant, the effect was small compared other drivers (Fig. 16). Age at out-migration gradually decreased with turbidity as juveniles chose to out-migrate sooner due to the increased difficulty of obtaining food. Age at out-migration also decreased with increased flow, as increased flow elevated predation risk thus lowering the size

Fig. 9 The relationships between the set of environmental drivers and the average distance from cover of juveniles. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

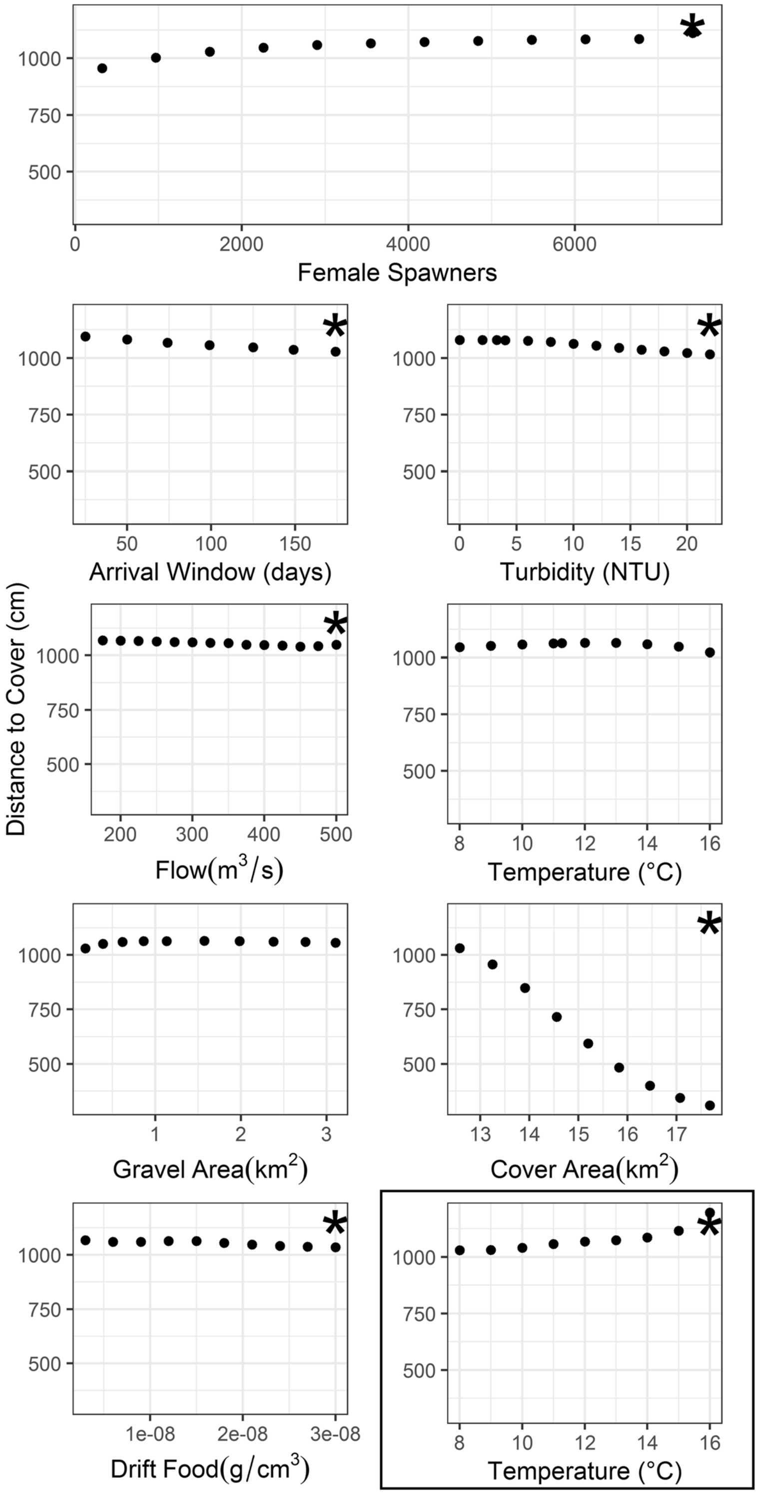


Fig. 10 The relationships between the set of environmental drivers and the juvenile risk of predation. I calculate predation risk by dividing the number of juveniles predation killed each day of the simulation by the total number of juveniles alive that day. I then take an average of those fractions weighted by the number of juveniles alive each day. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

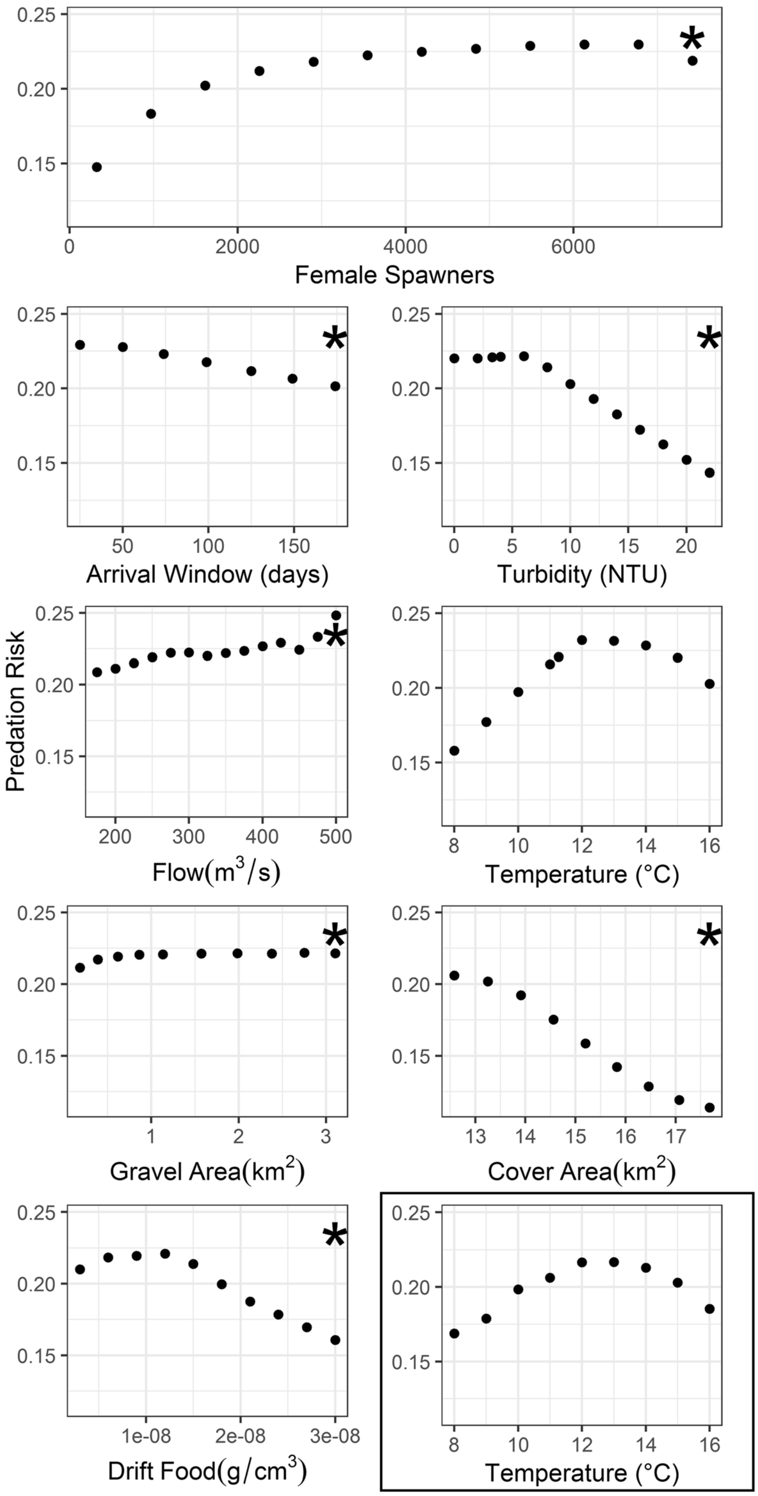


Fig. 11 The relationships between the set of environmental drivers and the average water velocity juveniles experience. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

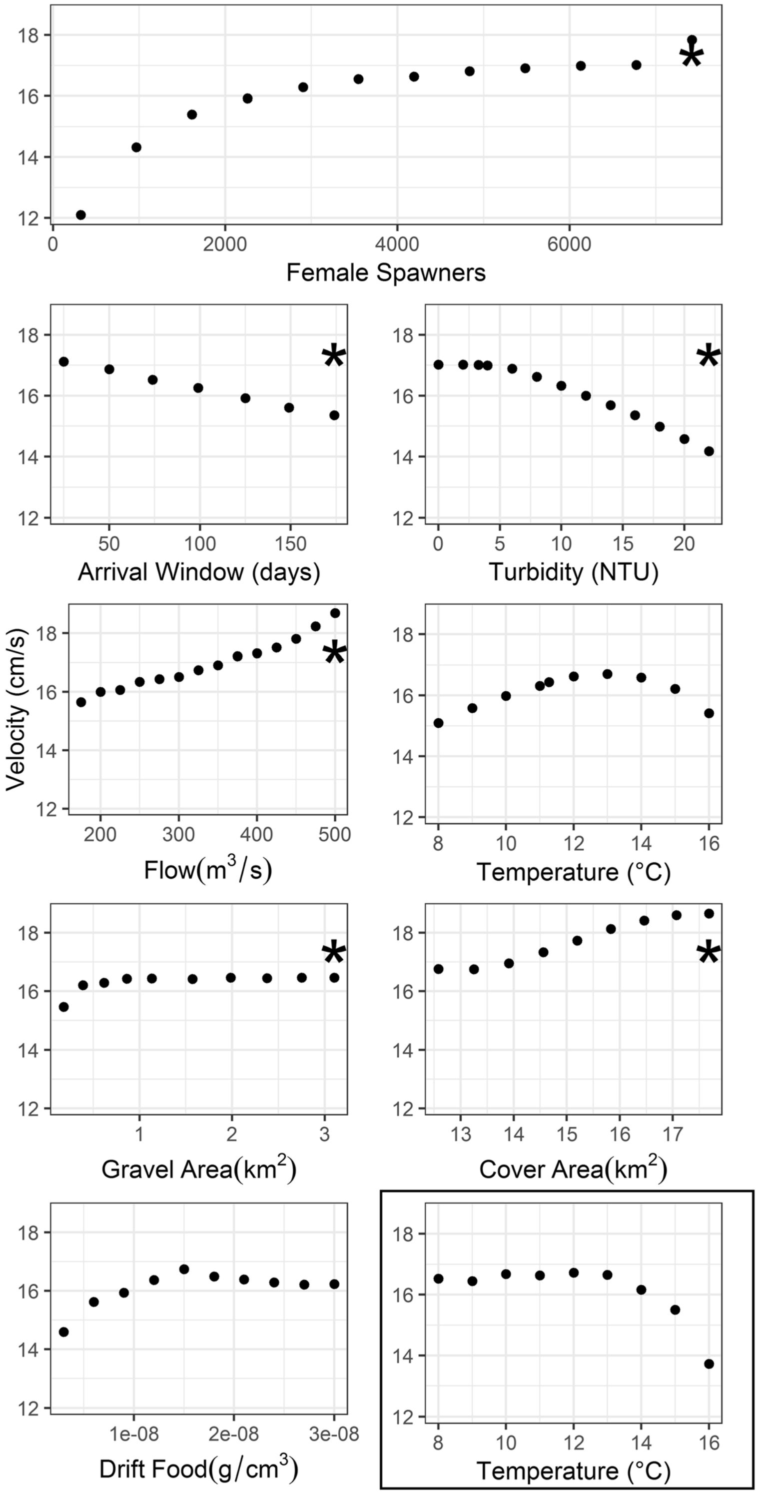


Fig. 12 The relationships between the set of environmental drivers and the average daily net energy use of juveniles. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

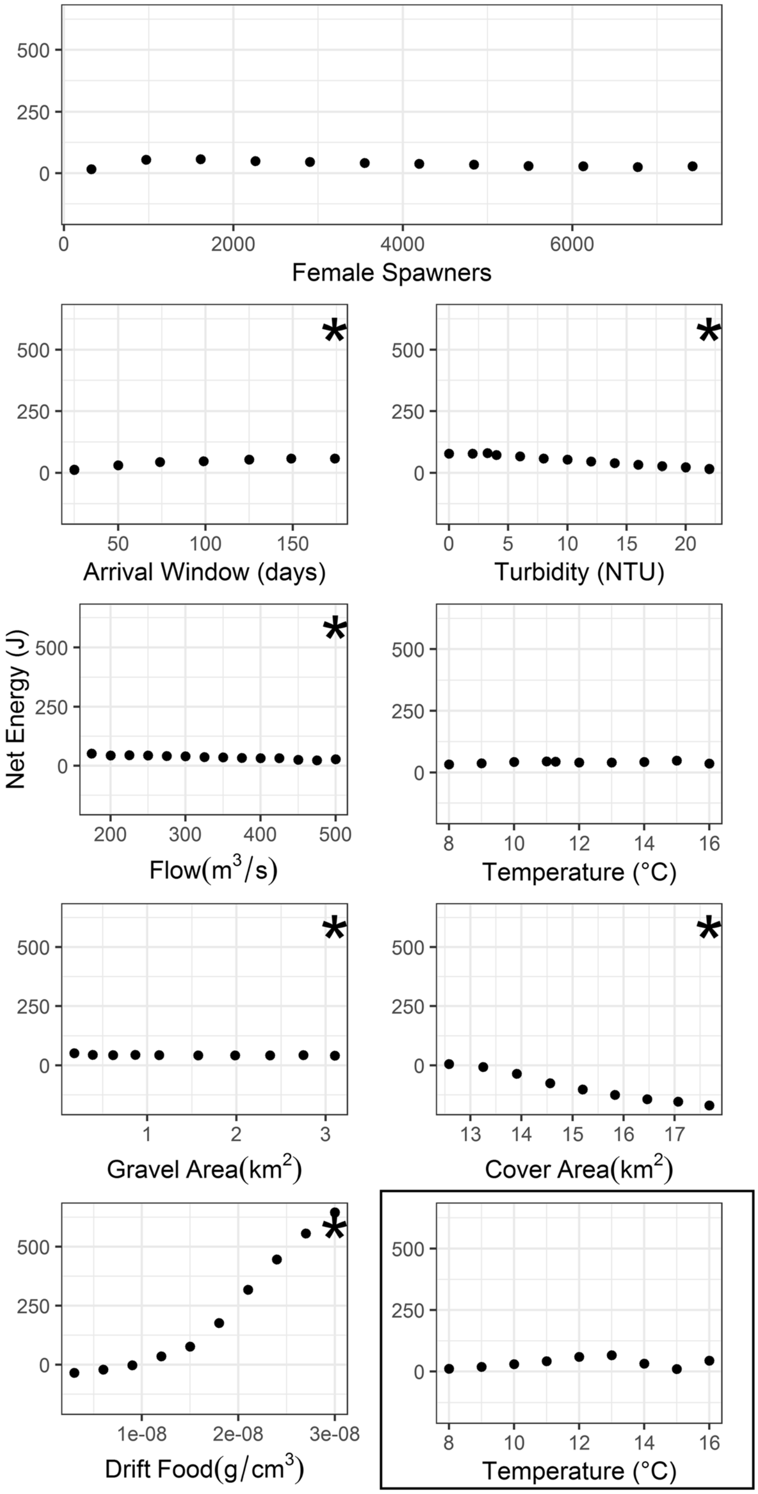


Fig. 13 The relationships between the set of environmental drivers and risk of poor condition mortality. As mortality from poor condition is not an instantaneous event but develops over time I analyzed this by dividing the number of poor condition mortalities from the whole simulation by the number of successfully emerged fry. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

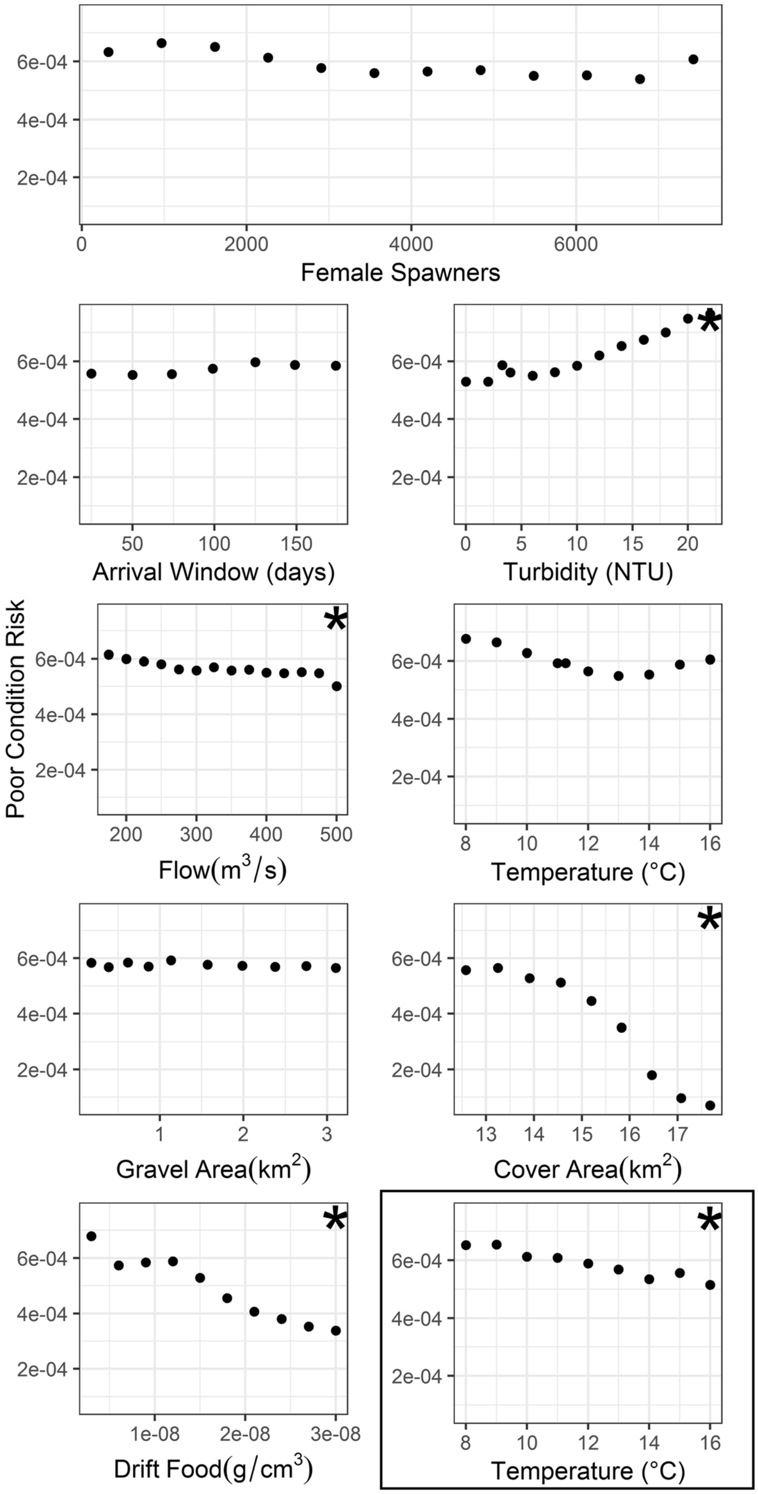
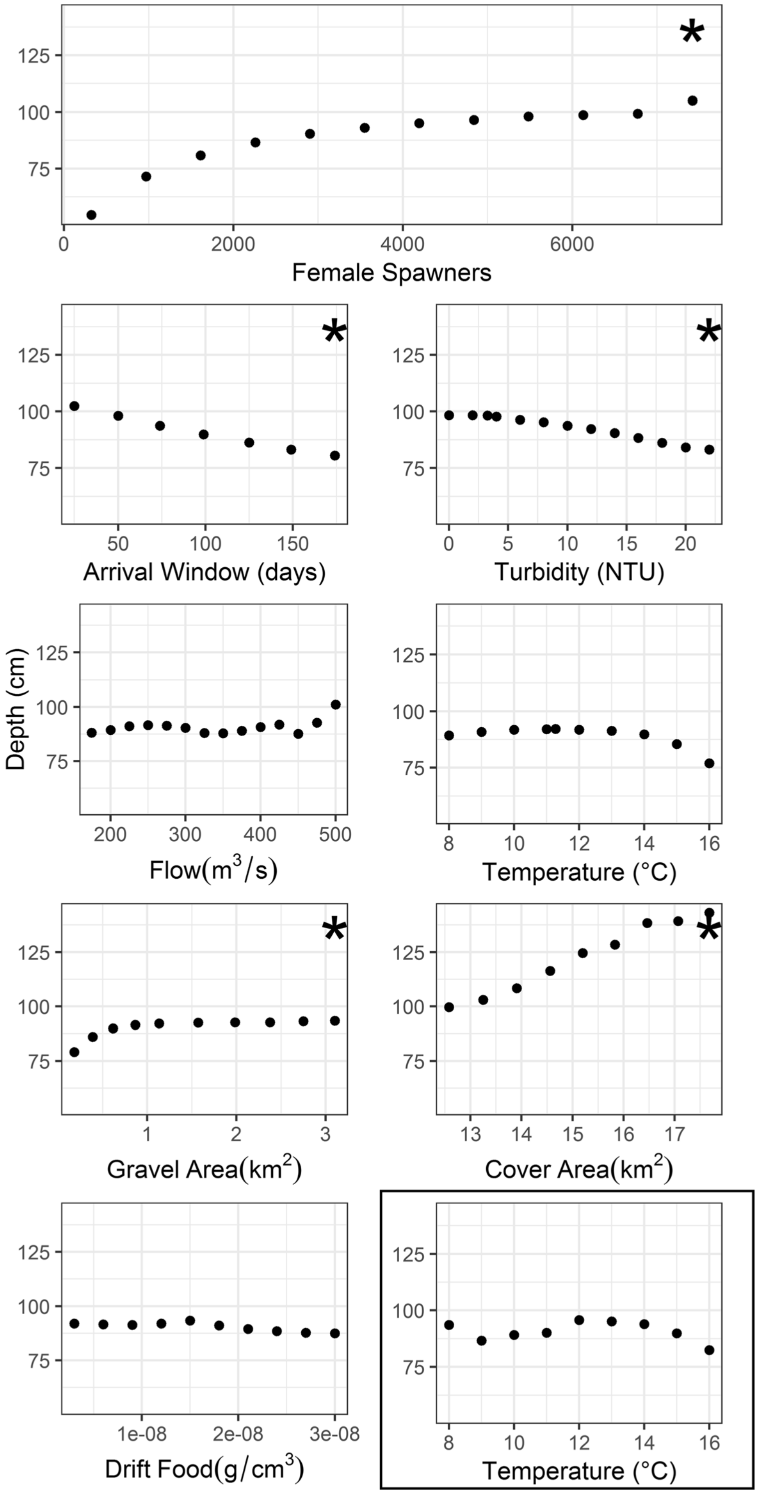


Fig. 14 The relationships between the set of environmental drivers and the average water depth juveniles experience. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction



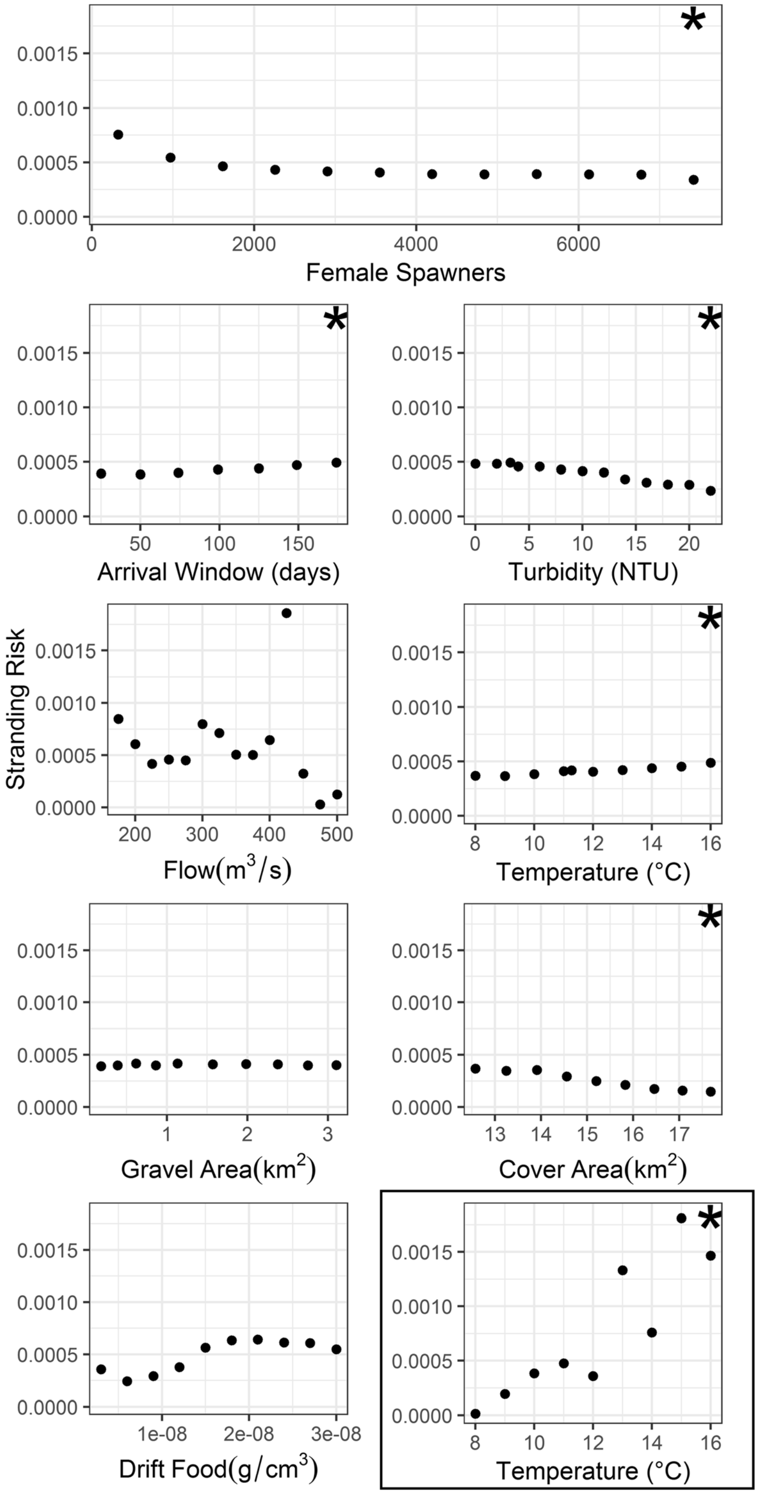
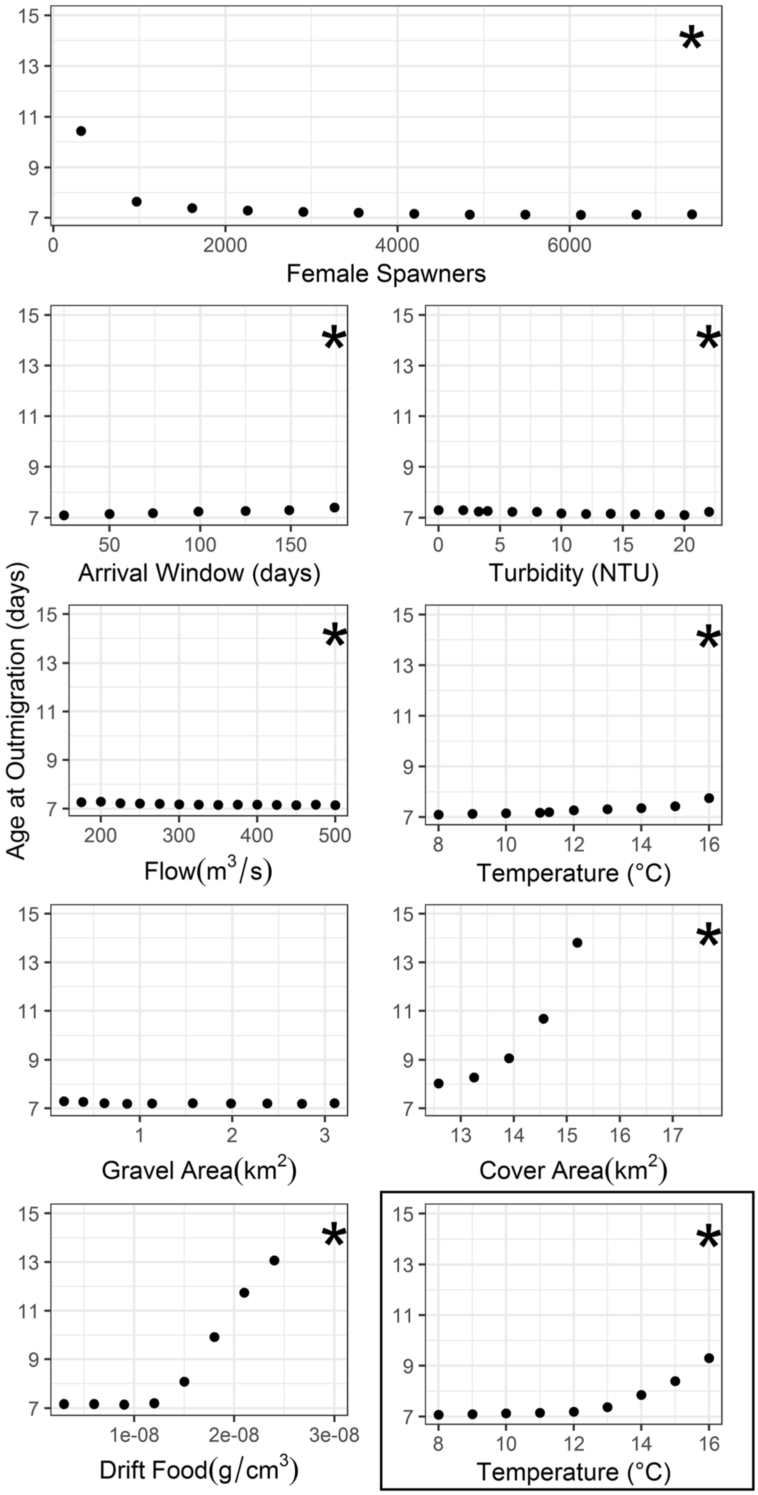


Fig. 15 The relationships between the set of environmental drivers and risk of stranding. I calculate stranding risk by dividing the number of fish stranding killed each day of the simulation by the total number of fish alive that day. I then take an average of those fractions weighted by the number of fish alive each day. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

Fig. 16 The relationships between the set of environmental drivers and the average age at outmigration. The bottom right plot is when temperature, flow and turbidity are changed in unison. Two points are not shown in the cover area plot so as to not extend the range of the y-axis too far to see details of other plots. The missing values are 36 and 36 days at 17.1 and 17.7 km^2 of cover respectively. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction



threshold to leave. At higher temperatures, there were fewer juveniles and the predation risk, while increasing, remained low so they stayed longer. Increasing concentrations of drift food allowed juveniles to stay longer and grow. When considering temperature, turbidity and flow, the effects of turbidity and temperature combined to overpower the effects of flow. The lower population simulations showed similar results (Appendix S1: Fig. S13).

Out-migrant count

More spawners caused subsequent juveniles to out-migrate faster, increasing the number of out-migrants per female up to a point after which the density dependent effects of superimposition and predation resulted in leveling off and a slow decline (Fig. 17). A longer arrival window resulted in lower density of juveniles, longer residence times, more predation (Fig. 10), and fewer outmigrants. Increased turbidity reduced the rate of predation, resulting in more out-migrants. Despite the many, and sometimes strong relationships between flow and other response variables mentioned above, there was only a small response in out-migrant count with increased flow. Increased temperature initially produced more risk of predation (Fig. 10) followed by significant egg mortality (Fig. 8). These two effects resulted in a continuous decrease in the number of out-migrants. There was still the artifact effect from gravel reducing superimposition (Fig. 7) present in the out-migrant count. Increased cover area allowed juveniles to stay longer and grow larger, but they were exposed to more predation (despite the per day risk of predation being lower), resulting in a lower out-migrant count. Once a minimum level of drift food was available, juveniles remained in the system; after which, addition food had little effect on out-migration count, resulting in no correlation. When considering temperature, turbidity and flow, temperature was the dominant mechanisms. There were similar relationships at the lower population level; however, some correlations switched in significance (Appendix S1: Fig. S14).

Out-migrant length

The negative density dependent relation with access to resources caused many small juveniles to out-migrate immediately, and the average size to decrease (Fig. 18). The arrival window had a similar relationship. Out-migration length showed a similar response to turbidity as age at out-migration (Fig. 16). Out-migration length decreased as turbidity and difficulty catching food increased. Increased flow caused juveniles to out-migrate faster and gave them less time to grow. Conversely, higher temperatures resulted in a longer time in the system and larger size. Cover area provided longer time to stay in the system and grow; however, the effect only occurred at higher values of cover. Increased drift food resulted in increased length. When considering temperature, turbidity and flow, turbidity and temperature were the dominate drivers and their effect was larger than either in isolation. There were similar relationships at the lower population level; except, there were no relationships between arrival window and out-migrant length at a lower population level (Appendix S1: Fig. S15).

Size class makeup

Increasing turbidity caused medium and large juveniles to decline quickly. Higher temperature left fewer juveniles in the system, resulting in an increase in large out-migrants. More cover allowed juveniles to stay secure in the system longer and grow, thus large juveniles replaced both small and medium juveniles. Increased drift food had little effect on small juveniles and a positive effect on medium and large juveniles, implying that large juveniles were not simply replacing small juveniles. When considering temperature, turbidity, and flow, turbidity was the dominate driver. There were similar relationships at lower population (Appendix S1: Fig. S16). Table 1 summarizes all the correlation relationships.

Discussion

This study quantifies many of the complex relationships that exist in a riverine system with a resident spawning

Fig. 17 The relationships between the set of environmental drivers and the number of out-migrants. The top graph is the relationships between the number of female spawners and the number of out-migrants per female spawner. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction

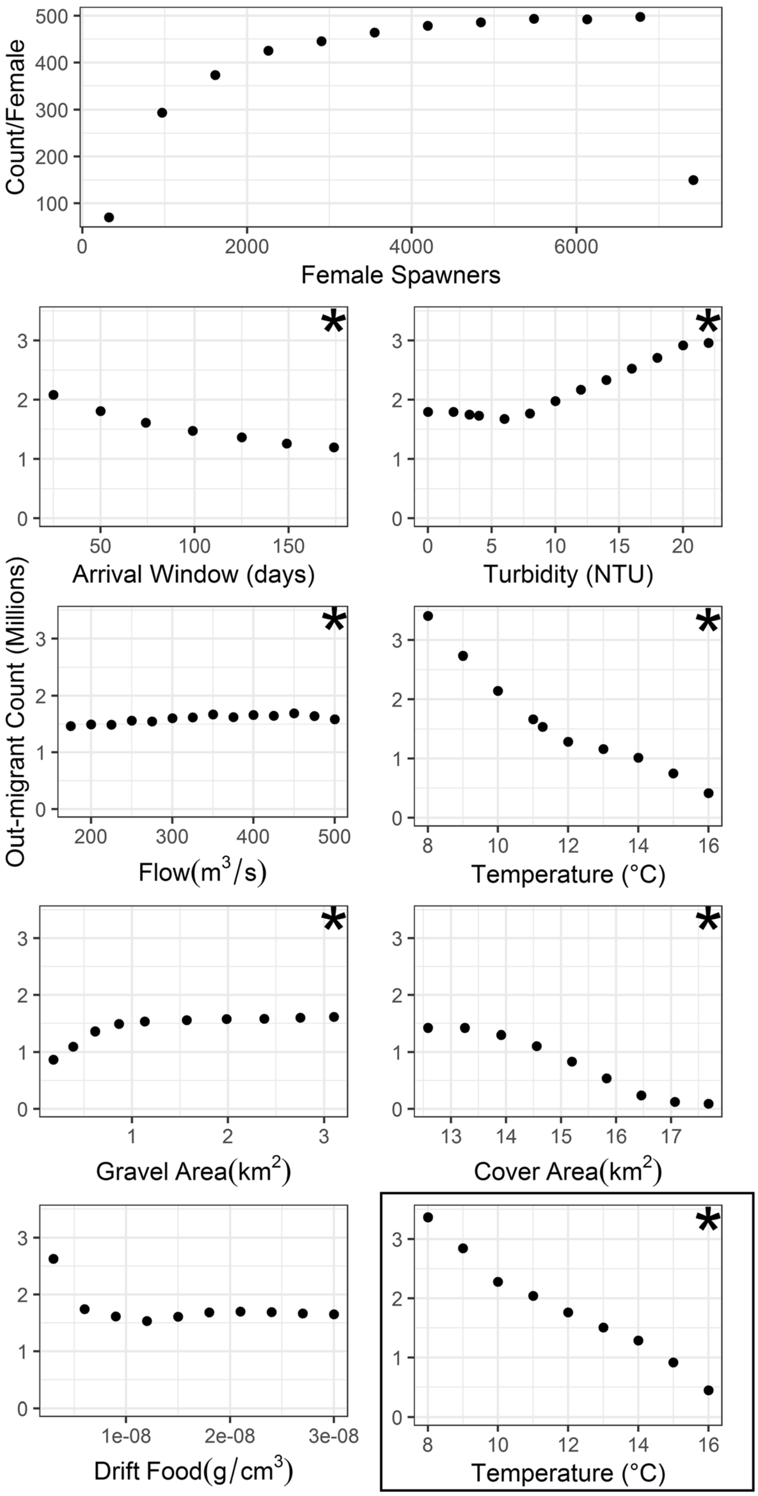
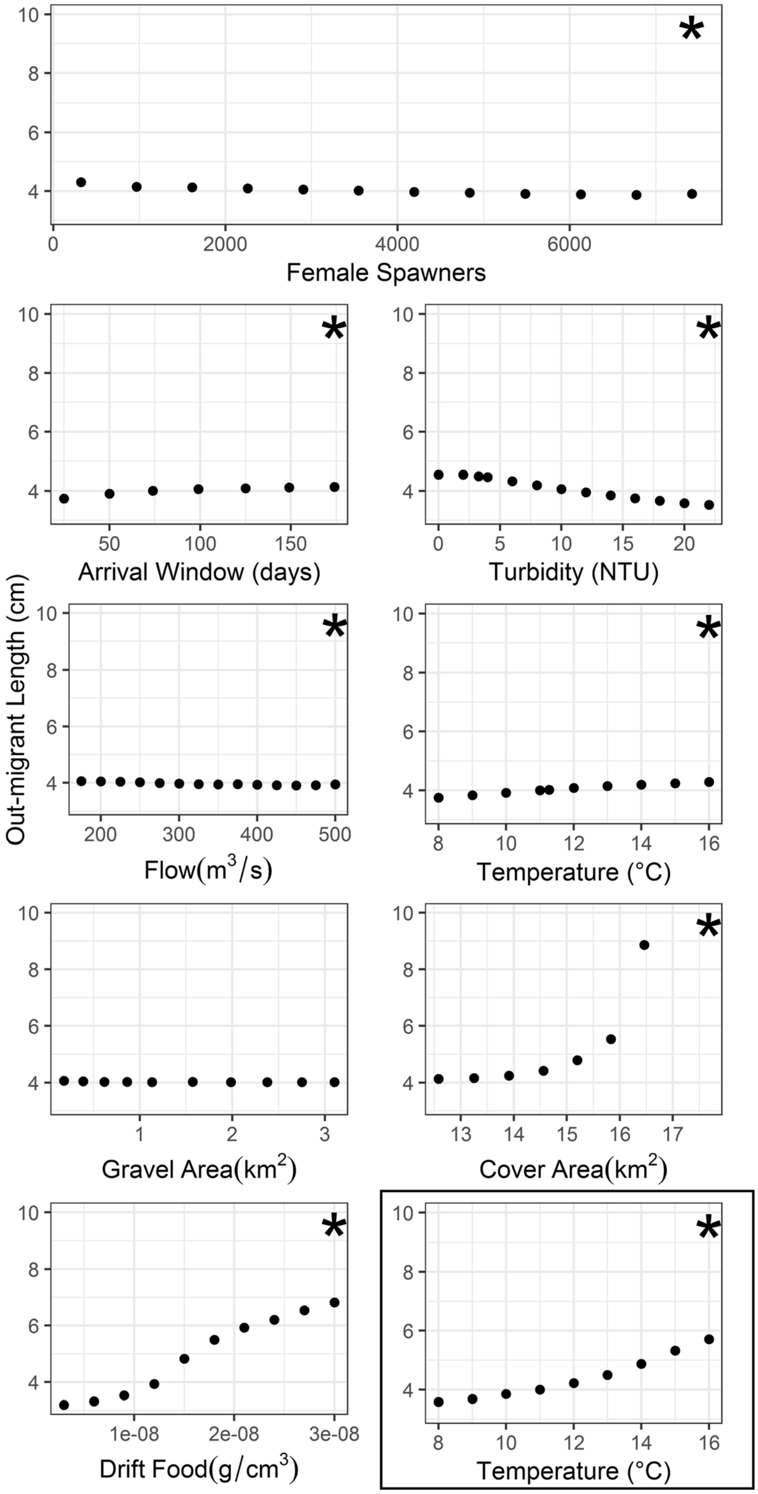


Fig. 18 The relationships between the set of environmental drivers and the average length of out-migrants. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction



fish population. Tracing the juvenile portion of the life cycle through these relationships results in the following general description. When a juvenile's parent enters the system, it has a higher chance of being spawning and hatching successfully under conditions of low flows, low spawner numbers, and high gravel area. High flows reduce adult stranding, but increase superimposition. During incubation, low water temperatures reduce egg mortality. Post hatching, predation is the greatest threat to juveniles, and they will attempt to find refuge either in shallow water, turbid water, or a location with physical cover. Lower juvenile densities result in better cover options per capita. Another defense to predation is to grow large quickly, and under low flow conditions there is increased access to food and reduced metabolic costs. Turbidity reduces growth by reducing feeding ability, but this negative impact is more than offset by directly reducing the risk of predation. Cooler water also reduces predation risks. Therefore predation risk is lowest for juveniles in cool, turbid, low flowing water. Compared to predation there is a much lower risk of poor condition and stranding mortality, which juveniles can reduce by moving into deeper waters. Poor condition is the only of the three juvenile mortality risks that is worse in turbid water, because it is harder to feed. While many of the drivers significantly affect stranding risk and poor condition, these sources of mortality remain minor compared to predation, which will determine the fate of most juveniles. Despite the historically low number of SRWRC simulated in this model, the fish still experience density dependent effects. The lower the density of juveniles in the system, the safer it is for a juvenile to stay longer and grow. If the density of juveniles per available cover area is high many juveniles will likely leave quickly. The factors impacting density dependence are number of spawners, superimposition rate, and temperature induced egg mortality. As juveniles migrate out, in all likelihood, they will be in the small size class, but they may be in the large size class if they encountered plenty of cover, low turbidity, and lots of food.

Looking at the system from a population perspective, at all but the lowest population levels, and unless there is a large amount of food, the cohort is dominated by small juveniles which cannot find a place to establish and grow in the upper river and therefore out-migrate immediately. Thus the changes in the average length of the out-migrants is often from adding or replacing some of the small juveniles with medium or large ones and not an overall increase in the size of juveniles in the small size class. Changes in the number of small out-migrants has the dominant effect on the out-migrants counts.

While small juveniles dominated the system population level dynamics, the IBM framework permits examination of other juvenile size classes, and larger juvenile classes likely have better survival farther down river. Interestingly, drivers which tended to increase the number of large and medium outmigrants also tended to decrease the total count of out-migrants. For example, as the cover area increased, the number of outmigrants decreased; however, the number of large outmigrants increased. Thus, detailed IBMs can reveal potential desirable outcomes for managers (more large juveniles) hidden within what appears to be a negative outcome (fewer juveniles).

The set of simulations where temperature, turbidity, and flow were varied together indicate that temperature was the dominant driver in most response variables, followed by turbidity and then flow. Looking at a summary of all drivers and their effects on the response variables also revealed some interesting phenomena (Table 1). Despite increasing predation rate and superimposition (the two main sources of mortality), higher flow rates increased the out-migrant count. More gravel reduced superimposition and had an effect on count, but did not affect the age nor the length of out-migrants. Increased food was not the dominant driver for any response variable, including length. Comparing the "lower population" to the "average population" results, seven response variables were significantly correlated in one set and not in the other. No response variable changed signs (positive to negative or vice versa) between sets. In general, they showed similar results with slight variation in the strength of the response.

Several of the relationships observed in the results are documented in the literature. Power et al. (1985) documented fish staying in shallower waters to avoid predation (Fig. 15). Mason (1976) found that populations counts were inversely related to size and that increased food in the system broke that relationship. I found a similar result for out-migration counts and out-migration lengths where there were inverse relationships, but not where drift food increased, then out-migration counts become stable after an initial decline (Figs. 17 and 19). Murphy (1985) showed that during a die off of pink

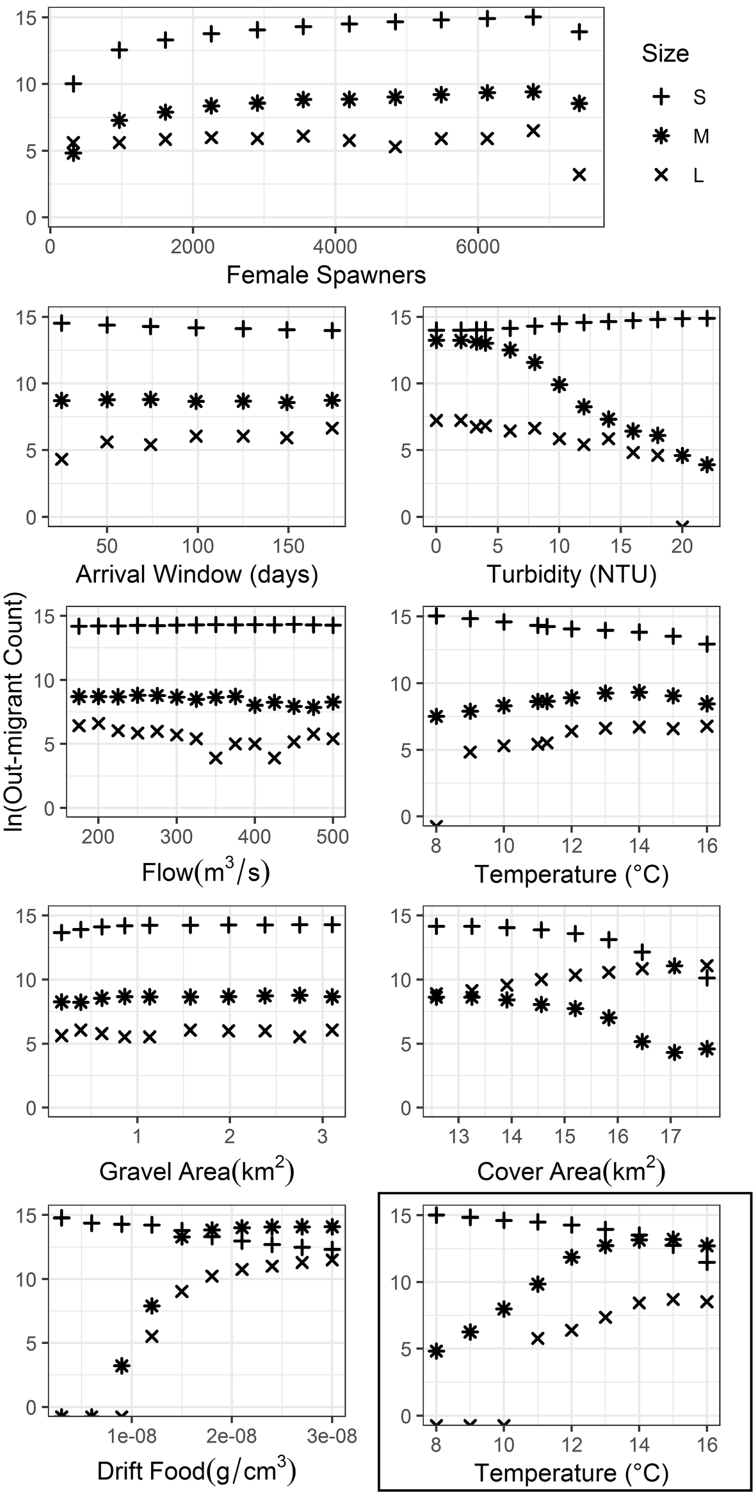
Table 1 A summary of the correlation tests between each driver and response variable. +, −, and 0 represent a positive, a negative, and no correlation respectively. Cells colored in black are the dominant driver(s) for a given response variable

	Pop.	Spawners	Window	Turb.	Flow	Temp.	Gravel	Cover	Food
Adult Stranding	Normal	0	0	0	–	0	0	0	0
	Low	NA	0	0	–	0	0	0	0
Superimposition	Normal	+	+	0	+	0	–	0	0
	Low	NA	+	0	0	0	0	0	0
Therm. Mort.	Normal	0	0	0	0	+	0	0	0
	Low	NA	0	0	0	+	0	0	0
Predation	Normal	+	–	–	+	0	+	–	–
	Low	NA	–	–	+	0	+	–	–
Poor Condition	Normal	–	0	+	–	0	0	–	–
	Low	NA	0	+	–	0	0	–	–
Stranding	Normal	–	+	–	0	+	0	–	0
	Low	NA	+	–	0	0	0	–	0
Age	Normal	–	+	–	–	+	0	+	+
	Low	NA	+	–	–	+	0	+	+
Count	Normal	+	–	+	+	–	+	–	0
	Low	NA	–	0	+	–	0	–	–
Length	Normal	–	+	–	–	+	0	+	+
	Low	NA	0	–	–	+	0	+	+

and chum salmon spawners, several died from stranding in shallow pools created from low flows (Fig. 6). Bilski and Rible (2010) showed not only that increasing density of spawners results in more superimposition but that the shape of the curve is similar to that seen when increasing gravel in these simulations (Fig. 7). Finally, Gregory and Levings (1998) found that turbidity reduced predation on migrating salmon (Fig. 10).

Beyond what is confirmed in the literature, many of the relationships observed in this study are expected, such as more drift food resulting in larger out-migrants, or more cover reducing predation; however, some results may not be intuitive. The lack of a relationship between increased flow and stranding is not intuitive, as increased flow should increase water depth and thus reduce stranding. Increased flows may simply open up more shallow pools while deepening others; however, the flow-predation relationship would suggest that is not the case. As mentioned above, the small effect of flow on the final count of out-migrants, despite it affecting four other response variables that affect salmon survival, is also not intuitive. While flow has a stronger effect on juvenile salmon counts at low densities, high densities may obscure the effects of flow on out-migrant counts. Thus, as the cohort of juveniles migrates farther down river and continues to shrink, the strength of flow's effect on the population count many increase. Another interesting result is the positive relationship between flow and superimposition, which is explained by the associated reduction in guarding time. In addition to producing interesting non-intuitive results, the simulations quantify the value at which there would be a diminishing return on gravel augmentation. Also, these simulations revealed which of two conflicting mechanisms is dominant when considering the arrival window and superimposition. As the arrival window lengthens, the density of spawners decreases but the number of ungraded nests increases. The effect of more unguarded nests is dominant.

Fig. 19 The relationships between the set of environmental drivers and natural log of the number of out-migrants in each size class. In the graph, a small out-migrant is under 5 cm, a large is over 8 cm, and in between is a medium. The bottom right plot is when temperature, flow and turbidity are changed in unison. An asterisk indicates that the variables were significantly correlated using Spearman correlation test with Bonferroni correction



While the trends these simulations produced will likely be applicable across many large river systems with resident salmonid populations, they may change and become invalid when looking at smaller river systems or anadromous fish with significantly different physiology or life histories. For example, smaller, less channelized rivers will have a different response to flow then the Sacramento River, or different species of fish may have tighter schooling behavior and thus have a muted response to adding more cover.

As with all modeled results, there is the potential for this type of analysis to misrepresent the extent to which drivers are influencing the system, and so it is important to ensure that the model is structured and parameterized with sufficient and relevant data as much as is possible. Additionally, there may be other important mechanisms that inSALMO currently does not consider. Of particular note, inSALMO currently does not account for disease, sedimentation in redds, the influence of temperature on food availability, gravel size for spawning, predation hot spots, or thermal refuges. As IBMs like these develop, more of these mechanisms should be included and tested to determine if, under certain conditions and in certain systems, our mechanistic understanding results in other drivers being dominant drivers of the systems.

Using an IBM, which is well parametrized and accounts for important drivers, to analyze interacting environmental drivers and responses of fish in a riverine system is an informative way to learn about the potential interplays of these drivers and responses. This paper demonstrates how an IBM can (1) quantify the individual driver effects on response variables, (2) quantify how those individual driver simulations compare to simulations where that driver is changed in unison with ones it is correlated with, (3) reveal complex size class structures that simple population models cannot, and (4) demonstrate how many of these drivers act through one response variable to influence another.

Acknowledgements I would like to thank Shawn Mayr and Todd Hillarie of CDWR for providing Sacramento River bathymetry, Andrew Pike for use of RAFT hindcasts, Benjamin T. Martin for comments on this manuscript, Eric Danner and Nathan Mantua for guidance in research and reviewing this manuscript, two anonymous reviewers for providing comments and the U. S. Bureau of Reclamation for funding.

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