



BRIEF COMMUNICATION

Warm winters and cool springs negatively influence recruitment of Atlantic salmon (*Salmo salar* L.) in a southern England chalk stream

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Abstract

Previous work suggests that juvenile salmon recruitment in rain-fed rivers is negatively influenced by warm and wet winters and cool springs. We tested whether this is generally applicable to a southern England chalk stream characterized by comparatively stable discharges and temperatures. We found that warm spawning and cool emergence temperatures negatively influenced juvenile recruitment between 2015 and 2020. Together these findings suggest an ability to predict juvenile productivity from water temperature records around spawning and fry emergence, thereby allowing time for management interventions in years of unfavourable temperatures.

KEYWORDS

climate change, productivity, salmonids, water temperature

Atlantic salmon *Salmo salar* L. (hereafter salmon) populations have declined in large parts of their distribution during recent decades (ICES, 2020). This decline has been largely attributed to reduced marine survival (Olmos *et al.*, 2019), although recent evidence suggests that the freshwater conditions experienced by juveniles affects their success at sea (Gregory *et al.*, 2019; Russell *et al.*, 2012; Tréhin *et al.*, 2021). Understanding and mitigating the broad-scale factors thought to regulate salmon survival at sea appears to be complex (Chaput *et al.*, 2020). Consequently, efforts to aid salmon population

recovery have strived to maximize juvenile productivity from their freshwater environment. If these efforts are to be effective, then we must understand the freshwater conditions that affect juvenile productivity.

In 2016, juvenile salmon numbers in England and Wales were among the lowest on record, and it was speculated that these were caused by an unusually warm winter and wet spring (ICES, 2017). A recent study presented evidence suggesting that winter and spring temperatures and discharges were associated with this

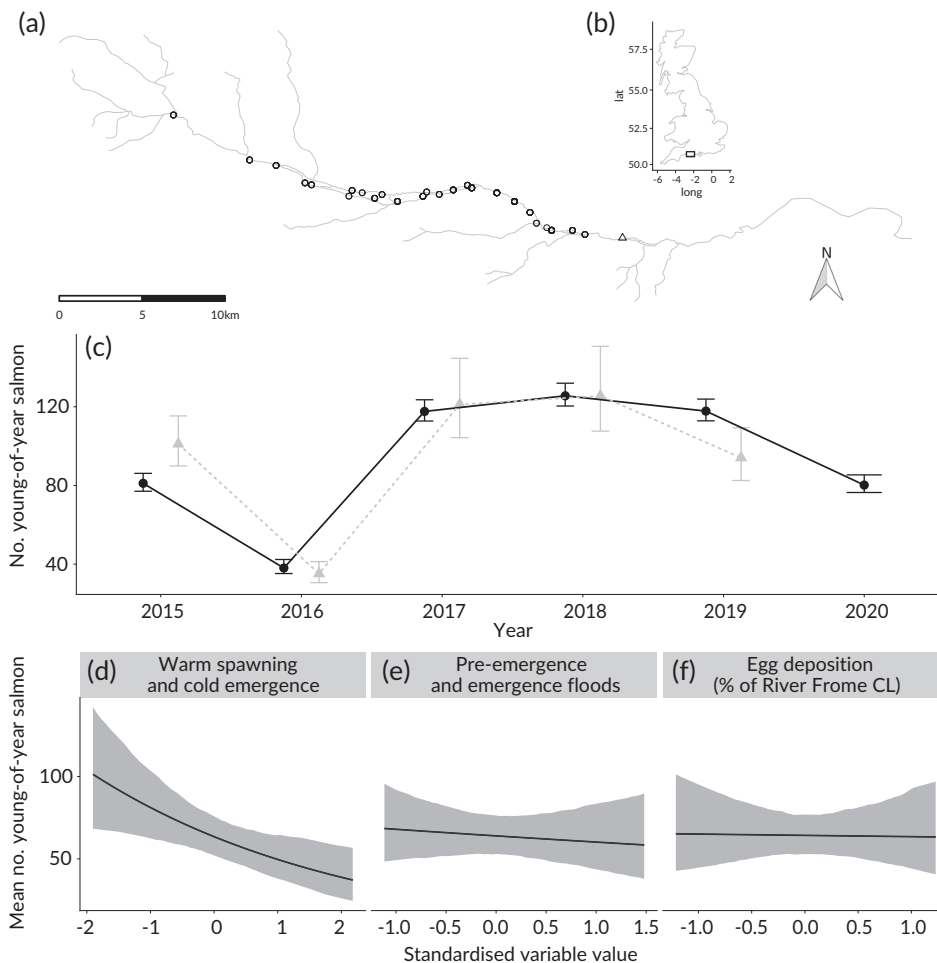


FIGURE 1 River Frome study sites: (a) location of the electrofishing density-sites (circles), temperature loggers and gauging weir (triangle) and (b) location in the UK, with (c) mean of model estimated site-specific juvenile salmon abundance and 95% credible intervals and mean catchment estimates of juvenile abundance and 95% confidence intervals (as smolt data is required for this estimate, data for 2020 parr could not be included. (—●—) mean site-specific estimate; (---▲---) mean catchment estimate/1000). Partial effects of (d) warm spawning and cold emergence, (e) pre-emergence and emergence floods, and (f) egg deposition on juvenile salmon abundance. The line represents the mean effect and the grey shaded area shows 95% credible intervals

‘2016 recruitment crash’ in seven rain-fed rivers throughout Wales (Gregory *et al.*, 2020). We observed similarly low juvenile abundance in 2016 on the River Frome, a primarily groundwater-fed chalk stream in southern England characterized by relatively benign temperature and discharge regimes (Berrie, 1992). Our study aims to test whether the findings from Welsh rivers are transferable to this chalk stream. Specifically, did temperature and discharge during spawning through to emergence influence juvenile population numbers between 2015 and 2020? Interestingly, this study period included 2020, when national juvenile salmon monitoring efforts were curtailed by the Covid-19 pandemic, but for which we also recorded low juvenile abundance on the River Frome, where monitoring efforts were unaffected.

The River Frome rises at Evershot (50°50′24″N, 02°36′12″W) and is c. 70 km long with an average gradient of 2.3 m km⁻¹ from its source to the tidal limit near Wareham (50°40′38″N, 02°07′30″W). Since 2015, 0+ juvenile salmon abundance (*i.e.*, young-of-the-year) has been surveyed at multiple sites across the catchment ($n = 21$ to 26; Figure 1a,b) using standardized k -pass depletion electrofishing surveys (Wyatt, 2002) in August and September. Note that there were too few older juvenile salmon to be considered in this study, as the majority of anadromous individuals migrate to sea after their first year in the river in this system

(Ibbotson *et al.*, 2013). All juvenile salmon captured in these depletion surveys, along with a large number of additional single pass surveys at sites throughout the catchment, were tagged with a Passive Integrated Transponder (PIT) tag. Together, these juvenile survey data are typically used to produce catchment-level abundance estimates, which are calculated from the number of juveniles tagged and their proportional occurrence among smolts captured during the following spring smolt run.

To test the influence of water and spring temperatures and discharges on juvenile abundance, we calculated explanatory variables representing spawning through to emergence temperature and discharge following Gregory *et al.* (2020). Specifically, we calculated temperature during spawning and emergence, and flood events during pre-emergence and emergence periods. These life history periods were defined from expert opinion and calculations (Table 1). We defined the spawning period as the last week of December to the third week of January, with the peak spawning date as 1 January following Gillson *et al.* (2020). Annually variable peak emergence dates were then calculated as a function of the peak spawning date and temperature. Using year-specific mean daily water temperature data, we calculated the theoretical peak emergence date as 820 degree-days after peak spawning (Edwards *et al.*, 2009; Table 1 and Supporting Information Figure S1). The emergence period began 2 weeks before and ended 4 weeks after

TABLE 1 Definitions of life-stage periods for each year calculated assuming 820 degree-days from peak spawning (1 January) to represent theoretical peak emergence

Year	Period			Theoretical peak emergence
	Spawning	Pre-emergence	Emergence	
2015	25 Dec to 21 Jan	23 Jan to 22 Mar	23 Mar to 04 May	06 Apr
2016	25 Dec to 21 Jan	23 Jan to 15 Mar	16 Mar to 27 Apr	30 Mar
2017	25 Dec to 21 Jan	23 Jan to 21 Mar	22 Mar to 03 May	05 Apr
2018	25 Dec to 21 Jan	23 Jan to 27 Mar	28 Mar to 09 May	11 Apr
2019	25 Dec to 21 Jan	23 Jan to 18 Mar	19 Mar to 30 Apr	02 Apr
2020	25 Dec to 21 Jan	23 Jan to 14 Mar	15 Mar to 26 Apr	29 Mar

the theoretical peak emergence for each year (Gregory *et al.*, 2020). The fry emergence period was judged to be longer than the spawning period because sedimentation typical of chalk streams (Riley *et al.*, 1998) can induce hypoxia, which can retard egg and embryo development (Bloomer *et al.*, 2016), and delay emergence until late April/early May (Riley & Moore, 2000). Pre-emergence covered the period between spawning and emergence.

We used daily discharge data recorded at the East Stoke gauging station on the River Frome (id: 44001) from the National River Flow Archive (<https://nrfa.ceh.ac.uk>; Supporting Information Figure S2). Following Gregory *et al.* (2020), a flood was defined as a high pulse when the discharge was between three and five times above the 50% (Q50) river level rate, and the number of floods during pre-emergence and emergence was calculated from the discharge data. We used River Lab Long Term Monitoring (RLTM) programme temperature data collected near the East Stoke gauging station (Supporting Information Figure S3) to calculate the mean water temperature during spawning and emergence. To test for any association between juvenile abundance and deposited egg numbers (a surrogate for density-dependence when data were considered too few to support a more complex density-dependence function), we used annual catchment-level estimates of egg deposition based on the size, sea-age and fixed sex ratios (probability of a returning adult being female for one-sea-winter = 0.41 and multi-sea-winter = 0.53) of returning adult salmon stock estimates from a resistivity fish counter and rod catch data (CEFAS, EA & NRW, 2019). These egg deposition estimates were expressed as a percentage of the river-specific conservation limit (Gregory *et al.*, 2020).

We used an N -mixture model (Kery & Schaub, 2012), where the observation model is represented by a k -pass depletion survey (Parent & Rivot, 2012; Wyatt, 2002). The abundance equation was given by:

$$\begin{aligned} N_{s,y} &\sim \text{Poisson}(\lambda_{s,y}) \\ \log(\lambda_{s,y}) &= \alpha + \beta \times X_y + \nu_{y:s} \\ \nu_{y:s} &\sim \text{normal}(0, \sigma) \end{aligned}$$

where $N_{s,y}$ is the abundance of juveniles at site s in year y , $\lambda_{s,y}$ is the expected number of juveniles at s in y given as a linear function of intercept α and a vector of coefficients β representing the effects of - year-specific explanatory variables in matrix X_y on $N_{s,y}$, and $\nu_{y:s}$ is a site nested within year random effect with variance σ . The

observation model was represented as a three-pass depletion survey given by:

$$\begin{aligned} C_{s,y,1} &\sim \text{binomial}(p, N_{s,y}) \\ C_{s,y,2} &\sim \text{binomial}(p, (N_{s,y} - C_{s,y,1})) \\ C_{s,y,3} &\sim \text{binomial}(p, (N_{s,y} - C_{s,y,1} - C_{s,y,2})) \end{aligned}$$

where $C_{s,y,1:3}$ are juvenile electro-fishing catches at s in y and in runs 1, 2 and 3, respectively, and p is the probability of catching an individual juvenile.

Before model fitting, all explanatory variables were z-standardized by subtracting their mean and dividing by their standard deviation and checked for collinearity using pairwise Pearson's correlations. A few pairs of explanatory variables were judged to be collinear ($r > |0.7|$ in Supporting Information Figure S4; Dormann *et al.*, 2013). Using principal components analysis, we reduced the correlated temperature and flood explanatory variables to orthogonal composite variables representing 'warm spawning and cold emergence' and 'pre-emergence and emergence floods', respectively. These composite variables and the egg deposition variable were statistically independent and used as the explanatory variables in the analysis (Supporting Information Figure S5).

Model parameters, namely α , β , σ and p , were assigned weakly informative priors and estimated by Monte Carlo Markov Chains (MCMC) using JAGS (Plummer, 2019). We made inferences based on 200 draws from three MCMC chains run for 20,000 iterations after 10,000 iterations of burn-in. Chains for all parameters were stationary and well-mixed, and had Rubin-Gelman statistic $\hat{R} \leq 1.1$ (Supporting Information Table S1 and Figure S6). Code to simulate data and reproduce the analysis are available in Supporting Information Figures S7 and S8.

Juvenile salmon abundance estimates varied annually, with the lowest number estimated in 2016 (Figure 1c) and these site-specific estimates appeared to successfully capture trends in catchment-level abundance estimates (Figure 1c).

High spawning temperatures and low emergence temperatures negatively influenced juvenile salmon abundance (Figure 1d and Supporting Information Table S1), corresponding with their influences on juvenile populations in Welsh rivers (Gregory *et al.*, 2020). Although chalk stream temperatures are relatively stable compared to rain-fed rivers, our findings suggest that changes in seasonal temperatures – even in chalk streams – have a detrimental influence on

juvenile salmon recruitment. This might be because effects of temperature are relative to local conditions and salmonid eggs are highly susceptible to increases in temperature (Elliott & Elliott, 2010). Relatively warm temperatures during spawning might also inhibit ovulation and affect gamete viability (Crisp, 1993; Taranger & Hansen, 1993). Cold temperatures during emergence might reduce feeding opportunities, negatively influencing growth and survival (Jonsson & Jonsson, 2009; Skoglund *et al.*, 2011).

Although the mean estimated effect of pre-emergence and emergence floods was negative, corresponding with Gregory *et al.* (2020) and studies throughout the UK (e.g. Gillson *et al.*, 2020; Millidine *et al.*, 2018), its influence on juvenile abundance in the current investigation was negligible (Figure 1e and Supporting Information Table S1). This suggests flood events in chalk streams are less influential in salmon recruitment relative to rain-fed rivers. This might be because chalk streams typically have a low gradient (Berrie, 1992) and flood events are unlikely to mobilize the redd substratum and cause egg washout or displace fry (Warren *et al.*, 2015).

There was no clear and simple association between egg deposition and juvenile abundance in these data (Figure 1f and Supporting Information Table S1), suggesting that the temperature and flow effects were sufficient to explain the interannual pattern in estimated juvenile numbers for these years. Although this appears to contrast with the findings of Gregory *et al.* (2020) that salmon abundance was negatively influenced by low and high egg deposition, this result could have been anticipated for several reasons (Mauder & Thorson, 2019), including (a) we analysed only 6 years of annual recruitment data, which included years of unusually high and low overwinter and emergence temperatures and floods when their influence might be expected to overshadow any weaker influences, (b) due to data constraints we only allowed for a simple association between egg deposition and expected mean juvenile abundance that might have been too simple (compared to more common density-dependence functions) to capture the true relationship, and (c) there are several other sources of known and unknown uncertainty, such as around the estimated female spawning escapements, that might mask any association or relationship between numbers of eggs and subsequent recruits.

Overall, our study suggests that environmental variables, particularly temperatures, influence the recruitment of juvenile (young-of-the-year) salmon. Previously, temperatures and discharge variables from spawning to emergence have been shown to influence salmon recruitment in seven Welsh rain-fed rivers (Gregory *et al.*, 2020) and here we show that the influence of temperature variables can be extended to a primarily groundwater-fed southern English chalk stream. Together, these results highlight how similar freshwater conditions in contrasting river-types have the potential to significantly affect juvenile salmon productivity and their subsequent population dynamics. This presents an opportunity to predict likely salmon recruitment immediately post-emergence, whilst it is still possible to manage the environment to promote survival of emerging juveniles. For example, maintaining aquatic vegetation to provide habitat and prey resources can maximize juvenile numbers in chalk streams (Marsh *et al.*, 2020). Unfortunately, owing to the confounding of

temperature variables in this study, we were unable to use our model to derive predictions under future climate change scenarios. However, disentanglement of the two temperature variables, which are less correlated over a longer period (Supporting Information Figure S9), might allow us to derive such predictions. An ability to make such predictions could be particularly important as climate change models predict an increased frequency of mild winters throughout the UK (UKCP09), such as those observed in 2016 and 2020.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Supplementary material

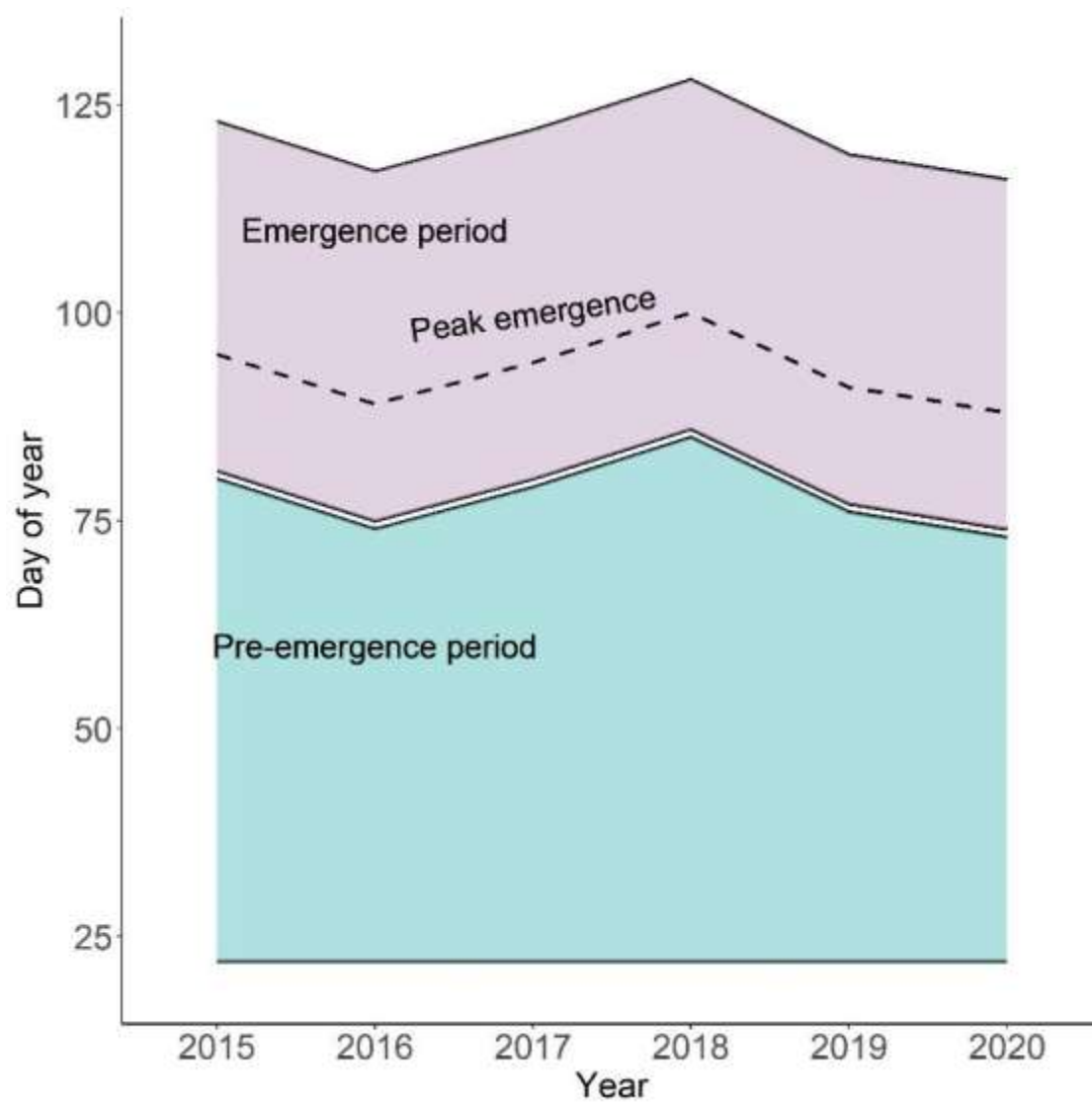


Figure S1: Plot showing annual timings of key life-stages in River Frome Atlantic salmon juvenile recruitment.

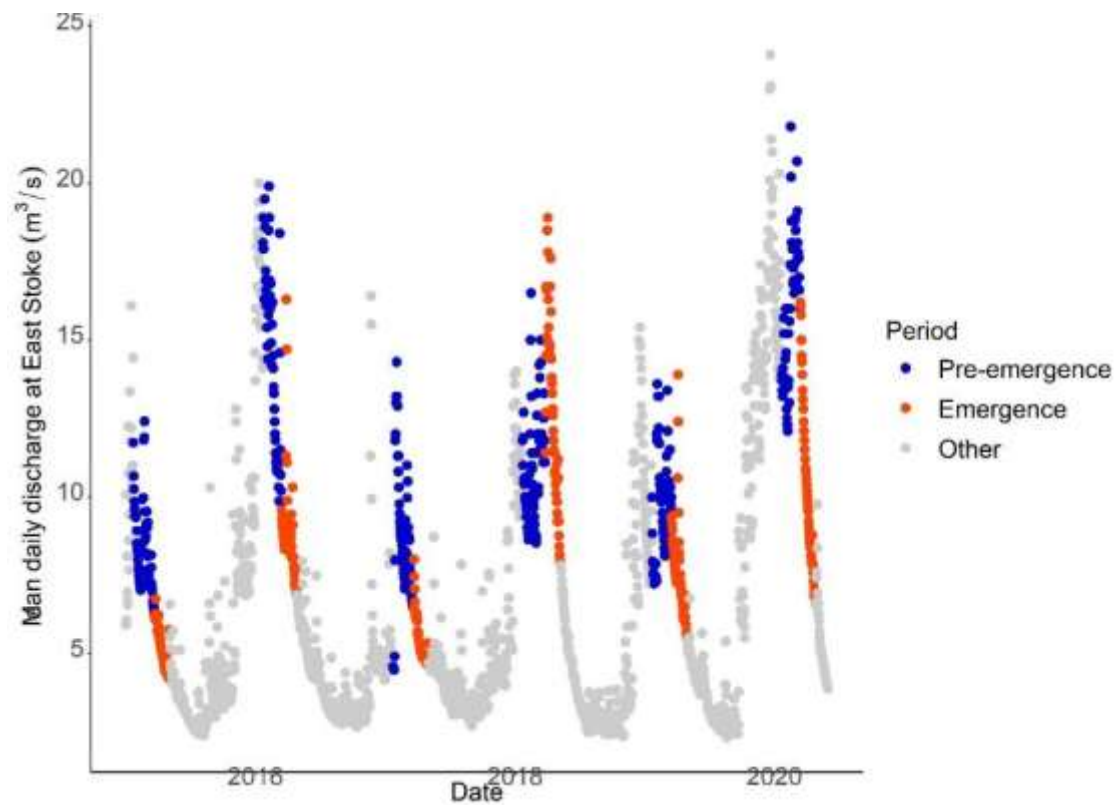


Figure S2: Raw mean daily discharge at East Stoke during the study period, dates which are included in the pre-emergence (blue circle) and emergence (orange circle) periods are shown for each year.

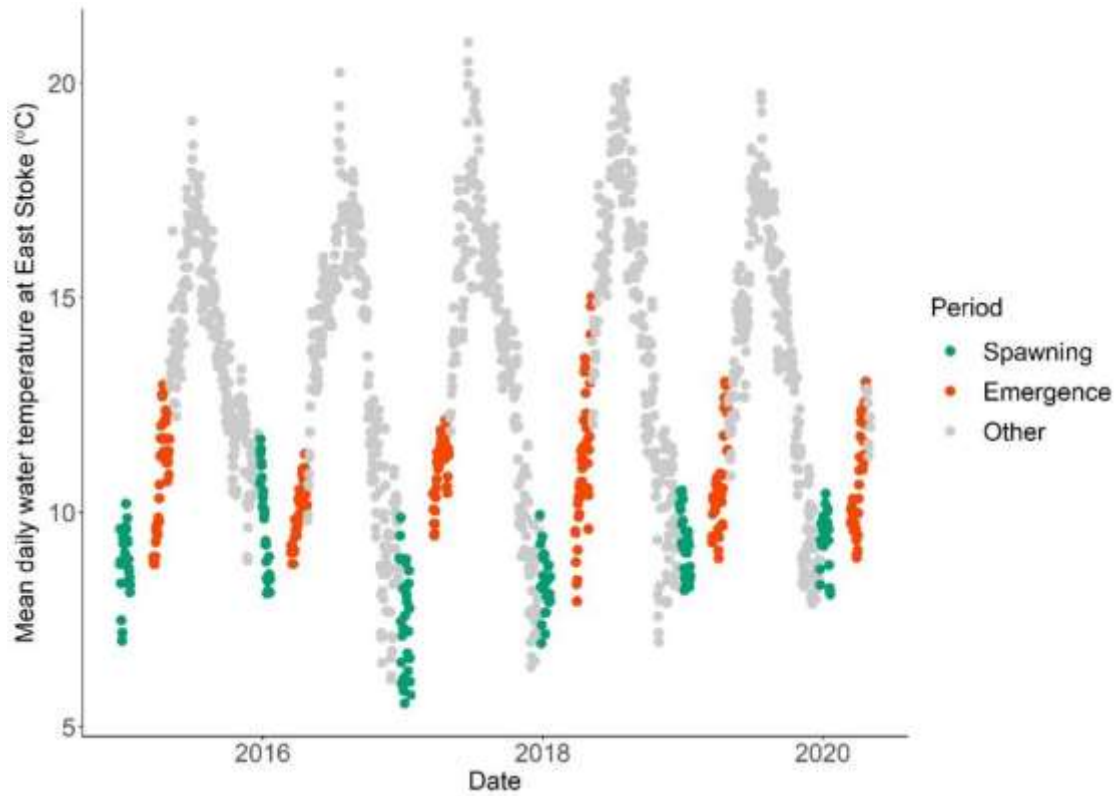


Figure S3: Raw mean daily water temperature at East Stoke during the study period, dates which are included in the spawning (green circle) and emergence (orange circle) periods are shown for each year.

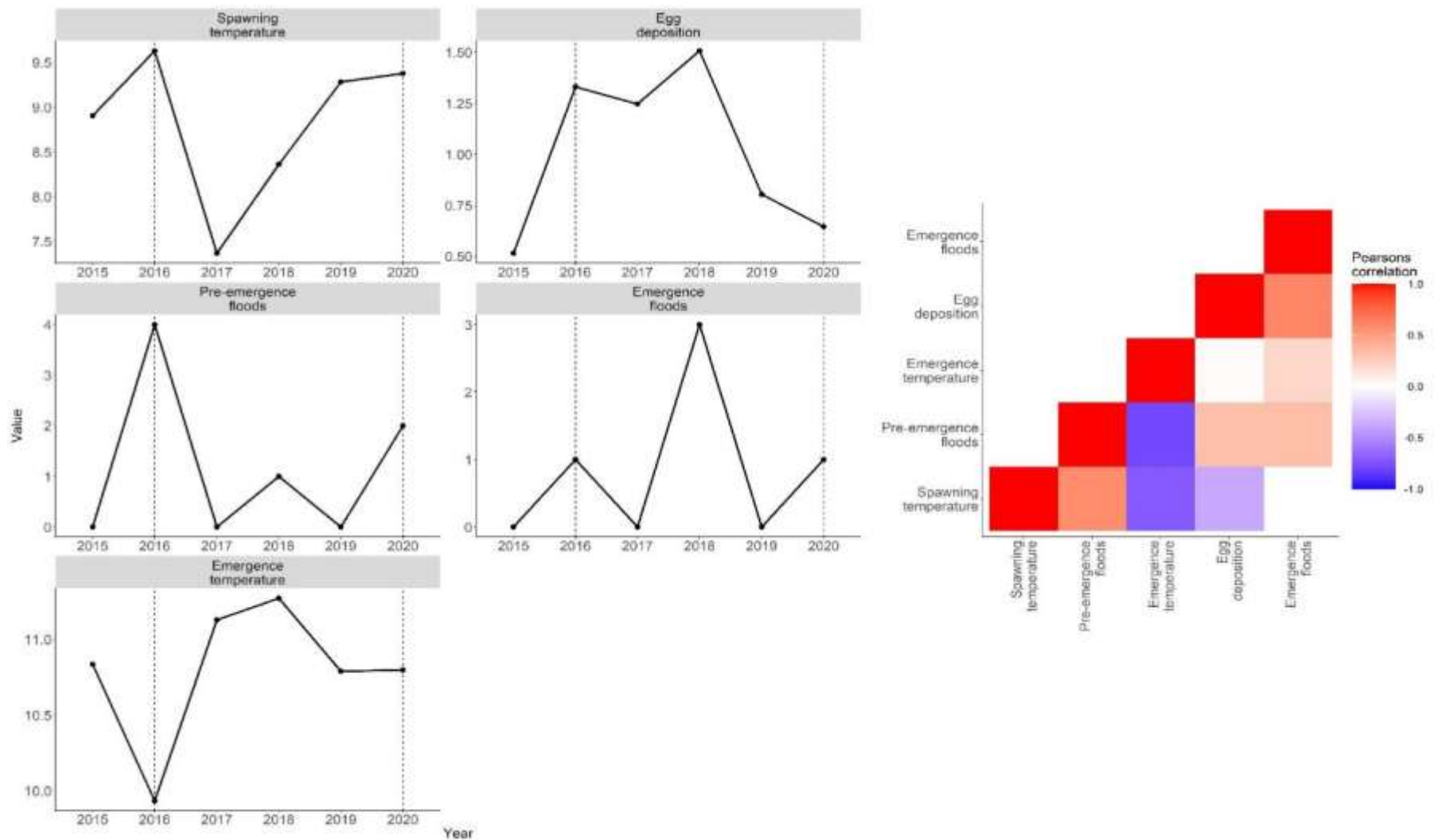


Figure S4: Plot showing all the initial explanatory variables derived to describe the annual juvenile salmon catches on the River Frome and the correlation matrix of all initial explanatory variables showing high (> 0.6) pairwise correlation coefficients between: emergence temperature and pre-emergence floods; emergence temperature and spawning temperature; and emergence floods and egg deposition.

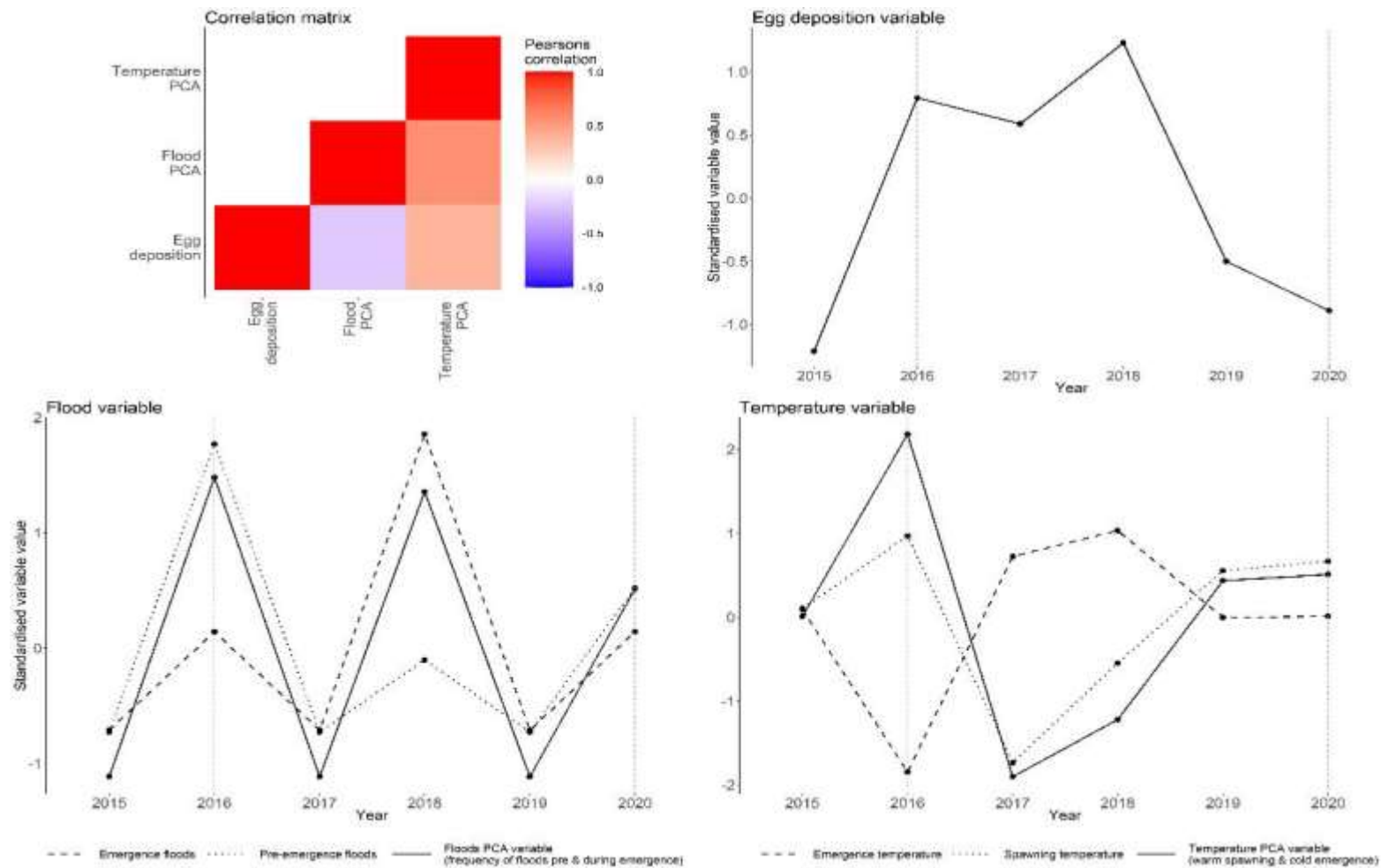


Figure S5: Summary of the final set of standardised explanatory variables tested in the parr abundance model, clockwise from top left: correlation matrix showing pairwise correlation coefficients that do not exceed $|0.7|$; annual estimates of egg deposition as a percentage of the River Frome conservation limit; the temperature variables - emergence and spawning temperature - combined using PCA to represent warm spawning and cold emergence periods; the flood variables - pre-emergence and emergence floods - combined using PCA to represent frequency of floods pre and during emergence.

Table S1. Model outputs. Mean coefficient estimates and 95% Bayesian credible intervals of model parameters, and Gelman statistic estimate to assess model convergence. An estimate of 1 suggests converged, stationary and well-mixing chains

Variable	Mean	2.5% Bayesian credible interval	97.5% Bayesian credible interval	Model convergence estimate
Intercept	4.14	3.97	4.31	1.01
Egg deposition	0.00	-0.30	0.29	1.00
Flood PCA	-0.07	-0.33	0.19	1.01
Temperature PCA	-0.24	-0.42	-0.06	1.01
Probability of capture	0.58	0.57	0.59	1.01
Year Site RE1	1.04	0.77	1.42	1.00
Year Site RE2	0.86	0.62	1.23	1.01
Year Site RE3	1.13	0.82	1.56	1.00
Year Site RE4	0.90	0.66	1.24	1.00
Year Site RE5	0.90	0.66	1.25	1.00
Year Site RE6	1.24	0.89	1.82	1.00

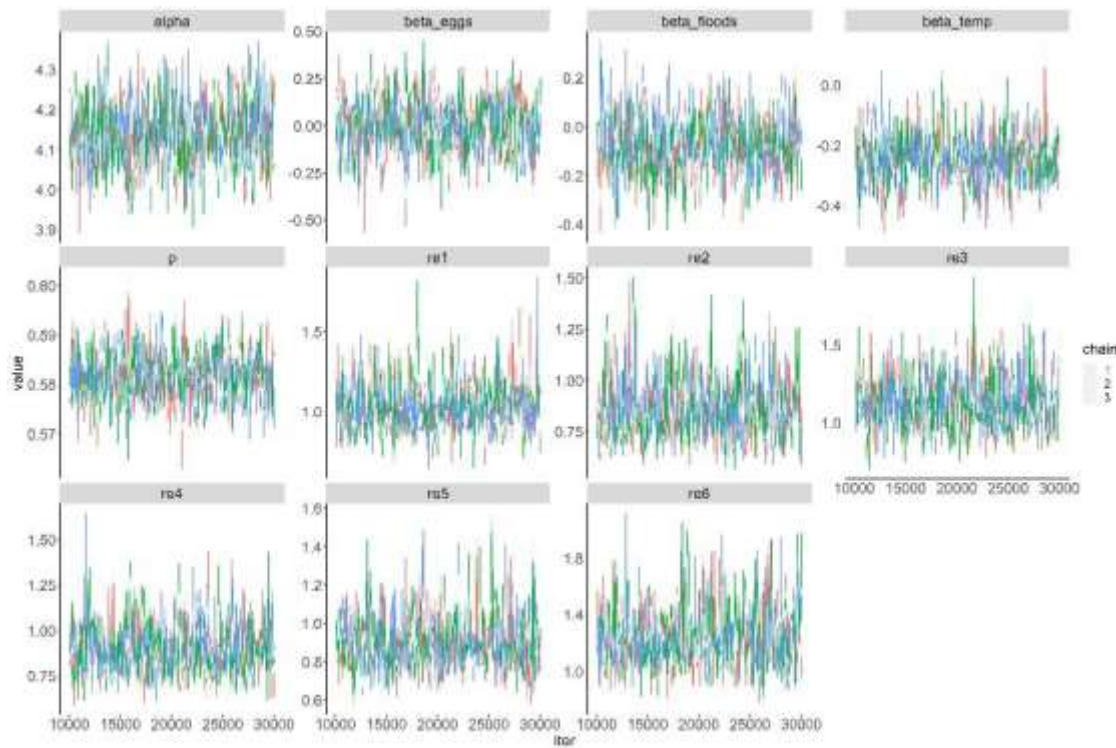


Figure S6. Trace plots for the estimated model parameters.

Simulation results

We simulated our analysis to ensure our model was well specified. We (1) specified values for some generating parameters (labelled in plots as “actual”), (2) used those generating parameters to simulate a realistic multi-annual and multi-site 3-pass depletion survey dataset using the same model that is used to estimate values of the parameters, (3) estimated the values of the generating parameters, and (4) plotted the results. Here is the code to reproduce the analysis and the results of one simulation run showing (1) for each generating parameter, the estimate compared to the actual value (Figure S7), and (2) the trace plots for each estimate (Figure S8).

```
# Set up -----

## start with clean workspace
rm(list = ls())

## main libraries
library(dclone, quietly = TRUE) # for jags fitting
library(data.table, quietly = TRUE) # for sample summarising
library(ggplot2, quietly = TRUE) # for plotting

# Simulate data -----

## specified as explicit and individual k-pass catches to allow for k = 1, 2
## or 3
## passes. If always k = 3, then can use multinomial in jags

## design parameters
nPasses <- 3 # "normal" number of passes - can be fewer
K <- nPasses + 1 # when using multinomial, this is the "fish remaining pass"
, i.e.,  $(1 - p)^3$ 
nYears <- 6 # what we plan to use from Frome data
nSites <- sample(5:22, nYears, replace = TRUE, prob = 5:22) # number of sites
per year
yrs <- rep(1:nYears, nSites) # needed for random effects
sts <- unlist(sapply(nSites, function(v) seq(1, v, 1))) # no of sites sampled
per year (not site-specific, i.e. a site within year number) - needed for ran
dom effects
n <- sum(nSites) # total number sites surveyed over all years

## sampling parameters
p <- 0.6 # probability of catching an individual; spatio-temporally invariant
pi <- c(p, (1 - p) * p, (1 - p)^2 * p, (1 - p)^3) # specify the probabilities
for the multinomial sampling

## simulate the abundance data
alpha_exp <- 5
alpha <- log(alpha_exp)
```

```

x <- rep(rnorm(nYears, 0, 1), nSites) # covariate of abundance
beta_x <- 1.5 # effect of covariate on abundance #1.25
beta_x2 <- -0.5 # -0.3
sd_nu <- sample(c(1, 1.5), nYears, replace = TRUE)
nu <- unlist(sapply(1:nYears, function(v) sapply(1:nSites[v], function(b) rnorm(1, 0, sd_nu[v]))))
lam <- exp(alpha + (beta_x * x) + (beta_x2 * x^2) + nu)
N <- rpois(sum(nSites), lam)

## catches; using Carle Strub removal
all_catches <- matrix(NA, nrow = n, ncol = K)
for (i in 1:n) {
  all_catches[i, ] <- rmultinom(n = 1, size = N[i], prob = pi)
}
catchs <- all_catches[, -K] # Discard final column of individuals not detected

## prepare catches
Catch <- data.table(catches)
colnames(Catch) <- paste0('Catch ', 1:3)

## remove some third runs; removing just one here to illustrate it works
Catch[2, 3] <- NA

## collate data
d <- data.table('Year' = yrs, # currently not used in analysis
               'Site' = sts, # currently not used in analysis
               'True abundance' = N,
               'Covariate' = x,
               'No Runs' = nPasses,
               Catch)

## view first and last 6 rows
print(head(d))
print(tail(d))

# Model fitting -----

## jags model function
f <- function() {

  # priors
  alpha_exp ~ dunif(0, 100)
  alpha <- log(alpha_exp)
  beta_x ~ dnorm(0, 0.01)
  beta_x2 ~ dnorm(0, 0.01)
  p ~ dunif(0, 1)

  # year:site random effect
  for(y in 1:nYears){

```

```

    tau_nu[y] ~ dgamma(0.01, 0.01)
    for(s in 1:nSites[y]){
      nu[y, s] ~ dnorm(0, tau_nu[y])
    }
    sd_nu[y] <- 1/sqrt(tau_nu[y])
  }

  ## model
  for (i in 1:n) {

    # abundance model
    mu[i] <- alpha + (beta_x * x[i]) + (beta_x2 * pow(x[i], 2)) + nu[year[i],
site[i]]
    log(lam[i]) <- mu[i]
    N[i] ~ dpois(lam[i])

    # observation model
    Catch[i, 1] ~ dbin(p, N[i])
    Catch[i, 2] ~ dbin(p, (N[i] - Catch[i, 1]))
    Catch[i, 3] ~ dbin(p, (N[i] - Catch[i, 1] - Catch[i, 2]))
  }
}

## data
d_l <- list()
d_l$Catch <- Catch
d_l$x <- x
d_l$n <- nrow(Catch)
d_l$nYears <- length(unique(d$Year))
d_l$nSites <- unname(table(d$Year)) # no. of sites sampled per year
d_l$year <- d$Year
d_l$site <- d$Site

## generating parameters
pars <- c('alpha', 'beta_x', 'beta_x2', 'N', 'p', 'sd_nu')

## monitors
mons <- c(pars)

## inits
inits <- function() list(N = rep(500, nrow(Catch)))

## debugging
if (0) {
  fii <- jags.fit(data = d_l, params = mons, inits = inits, model = f)
  stop()
}

## setup clusters

```

```

cl <- makePSOCKcluster(3)
parLoadModule(cl, 'lecuyer')
parLoadModule(cl, 'dic')
parLoadModule(cl, 'glm')

## jags fit
parJagsModel(cl = cl, name = 'res', file = f,
             data = d_l, inits = inits,
             n.chains = 3, n.adapt = 10000)
parUpdate(cl = cl, object = 'res',
          n.iter = 10000)
s <- parCodaSamples(cl = cl, model = 'res',
                  variable.names = mons,
                  n.iter = 20000, thin = 100)

## summarise fit
foo <- stack(s)

## create data.table
s_dt <- data.table(foo, keep.rownames = TRUE)
setkey(s_dt, variable, chain, iter)

## calculate the quantiles across chains
s_sum <- s_dt[, list(rn = rn[1],
                  mean = mean(value),
                  sd = sd(value),
                  min = min(value),
                  q025 = quantile(value, 0.025),
                  q25 = quantile(value, 0.25),
                  q50 = quantile(value, 0.50),
                  q75 = quantile(value, 0.75),
                  q975 = quantile(value, 0.975),
                  max = max(value)),
             by = list(variable)]
o <- order(as.numeric(s_sum$rn))
s_sum <- s_sum[o, ]
s_sum$variable <- factor(s_sum$variable, levels = s_sum$variable)

## remove variables
s_sum <- s_sum[, -'rn']

## stop cluster
parUnloadModule(cl, 'glm')
parUnloadModule(cl, 'dic')
parUnloadModule(cl, 'lecuyer')
stopCluster(cl)

## add actuals
foo <- unique(gsub('\\[[0-9]*\\]', '', s_sum$variable))
s_sum$actual <- unlist(sapply(foo, function(v) eval(parse(text = v))))

```



```

# Plotting -----

## coef plot
idx <- grep('^N\\[', s_sum$variable, invert = TRUE)
foo <- s_sum[idx, ]
fii <- foo[rep(1:nrow(foo), 2), list(variable, mean, q025, q975)]
fii$type <- factor(rep(c('estimate', 'actual'), each = nrow(foo)))
fii[type == 'actual', 'mean'] <- foo$actual
fii[type == 'actual', 'q025'] <- NA
fii[type == 'actual', 'q975'] <- NA

coef_p <- ggplot(fii, aes(x = variable, y = mean, colour = type)) +
  geom_errorbar(aes(ymin = q025, ymax = q975), width = 0.25, size = 1.25) +
  geom_point(size = 5) +
  ylab('estimated value') +
  xlab('variable')
print(coef_p)

## trace plots
idx <- grep('^N\\[', s_dt$variable, invert = TRUE)
foo <- s_dt[idx, ]

trace_p <- ggplot(foo, aes(x = iter, y = value, colour = chain)) +
  geom_line() +
  facet_wrap(~ variable, scales = 'free_y') +
  theme(axis.text.x = element_blank())
print(trace_p)

```

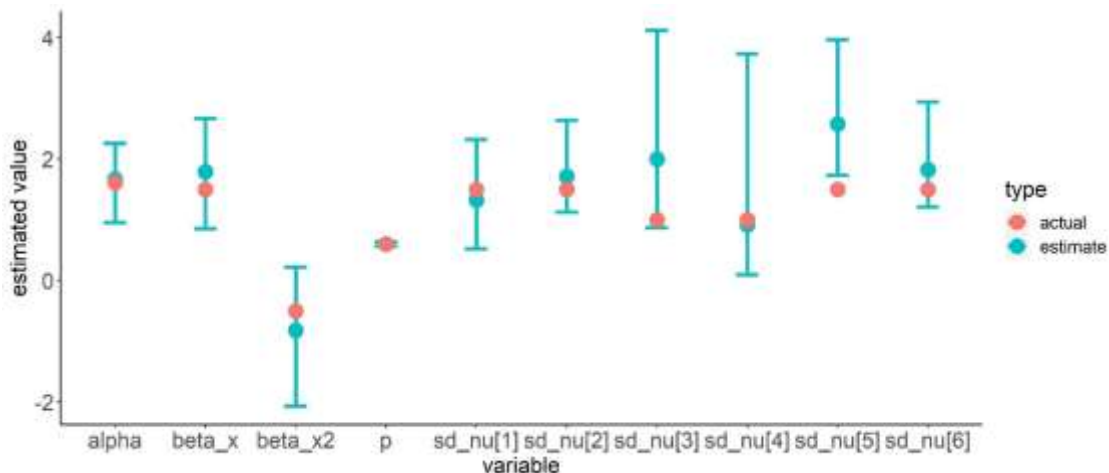


Figure S7: Plot of estimated coefficient values compared to the actual values used to simulate the data.

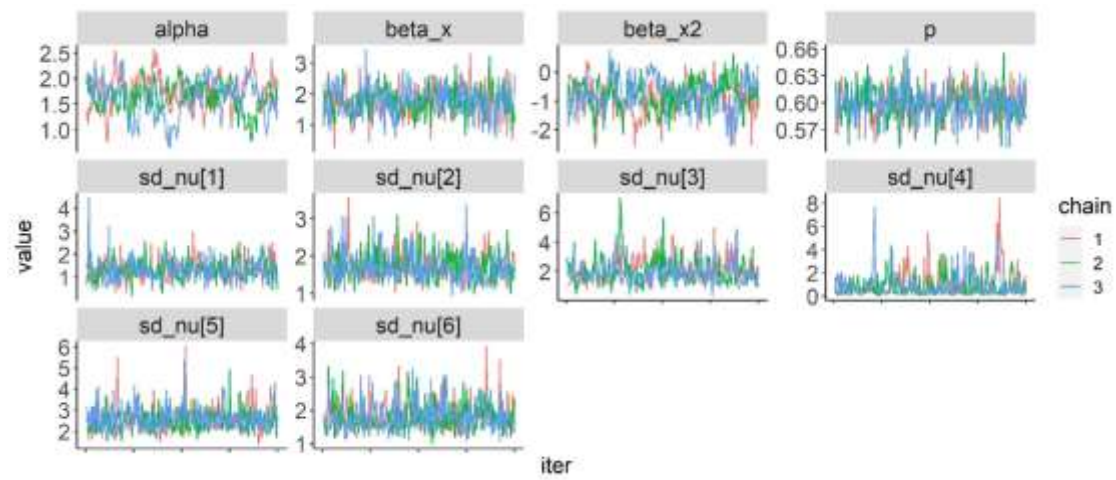


Figure S8: Trace plots for the estimated coefficients.

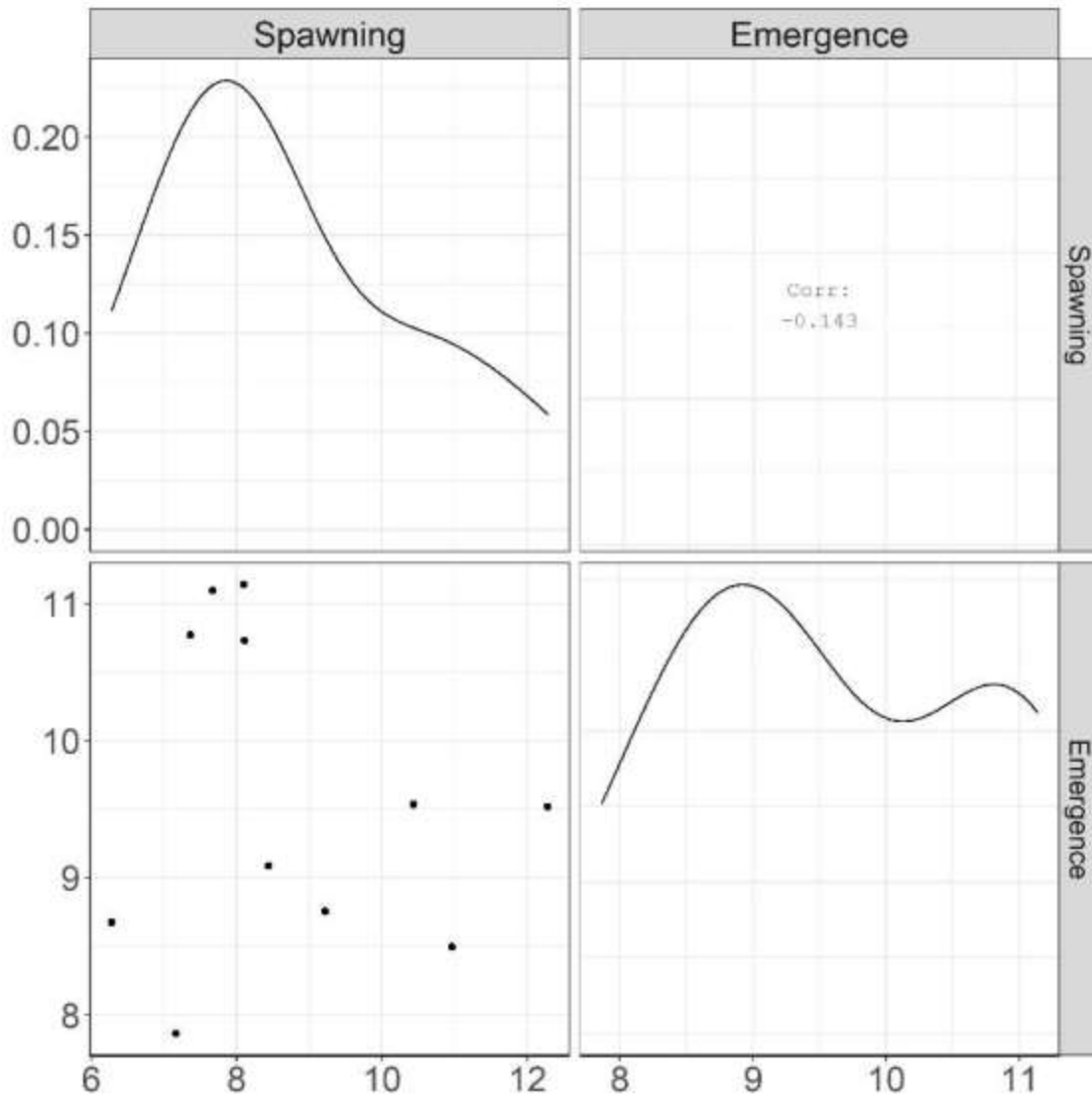


Figure S9: Correlation between mean temperature during spawning and emergence periods for an extended time-series (2009-2020). Clockwise from top left: frequency histogram of spawning temperature data; Pearson's correlation coefficient between spawning and emergence temperature data; frequency histogram of emergence temperature data; raw data points for each year ($n = 11$).