Is recruitment of brown trout in a New Zealand river driven by parental spawning investment, density dependence, or environmental factors?

Pavel Mikheev[1,2], Christoph Matthaei[3], Travis Ingram[3], Matt Jarvis[3], and Gerard Closs[3]

[1]Department of Zoology of Vertebrates and Ecology, Perm State University,
ul. Bukireva, 15, Perm, 614068, Russian Federation
[2]Russian Federal Research Institute of Fisheries and Oceanography, Khabarovsk Branch,
Amurskiy bul., 13a, Khabarovsk, 680038, Russian Federation
[3]Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand

Address correspondence and requests for materials to Pavel Mikheev, pmikheev@yandex.ru

Abstract

This study addresses the primary factors driving young-of-the-year (YoY) brown trout *Salmo trutta* abundance and population dynamics through the Austral summer in an important spawning tributary of a large New Zealand river. We measured the key traits and spawning investment of spawners; YoY density and movement; and environmental characteristics important for juvenile trout. In comparison to their native European range, we found high rates of pre-spawning mortality, low density of deposited eggs and reduced spawning efficiency of adult brown trout. Parental spawning investment did not affect spring juvenile trout distribution, a result likely related to a mismatch between YoY abundance and densities of eggs deposited by adults at the sampled locations. Spatial differences in seasonal dynamics of YoY density were likely related to the diversity of environmental conditions affecting habitat suitability for post-larval brown trout along the stream. Significant correlations between juvenile trout loss rate and both YoY density and downstream migration were observed only for the lowland stream segments, which had the highest spawning investment from diadromous adults, indicating the importance of these locations for recruitment. This study highlights knowledge gaps in species-environment interactions and the reproductive ecology of brown trout in New Zealand.

Keywords: *Salmo trutta*, life histories reproduction, recruitment, density-dependence, spawning mortality

Introduction

Understanding the major factors driving the temporal dynamics of the abundance of species is the key focus of many ecological studies (Mutshinda, O'Hara and Woiwod, 2009; Ye and Carocci, 2019). The primary mechanisms controlling abundance can be separated into two classes: environmental and endogenous. External environmental drivers are often more important in regulation of population dynamics at the periphery of species distribution, where density varies in accordance with the key environmental conditions (Bjørnstad and Grenfell, 2001; Gou et al., 2005; Dahlgren, Bengtsson and Ehrlén, 2016). Endogenous control occurs mainly when density-dependence drives the population to equilibrium at the core of distribution where variability of important environmental factors is low, and the long-term abundance values tend to balance close to carrying capacity (Dennis and Trapper, 1994; Murdoch, 1994; Jenkins, Diehl, Kratz and Cooper, 1999; Huntsman and Petty, 2014).

Brown trout *Salmo trutta* exhibit remarkable phenotypic plasticity and are a popular model for testing both density-dependent and environmental mechanisms regulating the population dynamics of wild fish (Elliott, 1994; Jonsson and Jonsson,

Citation: Mikheev, P., Matthaei, C., Ingram, T., Jarvis, M., and Closs, G. 2022. Is recruitment of brown trout in a New Zealand river driven by parental spawning investment, density dependence, or environmental factors? Bio. Comm. 67(3): 203–216. https://doi.org/10.21638/spbu03.2022.306

Authors' information: Pavel Mikheev, PhD, Leading Researcher, orcid.org/0000-0002-0934-6935; Christoph Matthaei, PhD, Professor, orcid.org/0000-0002-4823-9198; Travis Ingram, PhD, Senior Lecturer, orcid.org/0000-0003-0709-5260; Matt Jarvis, PhD Student, orcid.org/0000-0001-8276-1097; Gerard Closs, PhD, Professor, orcid.org/0000-0003-4550-6024

Manuscript Editor: Pavel Skutschas, Department of Vertebrate Zoology, Faculty of Biology, Saint Petersburg State University, Saint Petersburg, Russia

Received: April 22, 2022;

Revised: May 11, 2022;

Accepted: June 21, 2022.

Funding: This study was funded by a University of Otago Doctoral Scholarship awarded to Pavel Mikheev.

Ethics statement: The research was approved by Otago University Animal Ethics Committee (permission 56/2016).

Competing interests: The authors have declared that no competing interests exist.

2011; Lobón-Cerviá and Sanz, 2017). The ecological flexibility of brown trout is a major contributor to its popularity as a sport fish, with the species being introduced to many areas outside its native European range, and is now widely established in both the Northern and Southern hemispheres. Multiple studies have focused on the factors controlling stream-dwelling brown trout in a variety of geographical regions and habitats, but the results are often contradictory and generate more questions than answers (Lobón-Cerviá, Rasmussen and Mortensen, 2017). In New Zealand there are few studies of the population dynamics of brown trout (Allen, 1951; Kristensen and Closs, 2008a; Hayes, Olsen and Hay, 2010; Jones, Akbaripasand, Nakagawa and Closs, 2019), and one study has examined their migration dynamics (Holmes et al., 2014). The effects of natural reproduction, food abundance, floods and other environmental factors on trout population dynamics in New Zealand were analyzed by Hobbs (1940, 1948), Allen (1951), Burnet (1959), Jowett (1989, 1990, 1995) and Hayes (1995), with the importance of different factors in driving brown trout populations in New Zealand being a source of long-standing debate (Huryn, 1996; Holmes et al., 2018).

Previous studies have determined that the broad scale spatial population dynamics of young-of-the-year (YoY) brown trout are closely related to the dominant life history traits of adults. Populations in river reaches accessible to large diadromous adults are characterized by high juvenile densities and unstable population dynamics (Kristensen et al., 2011; Jones, Akbaripasand, Nakagawa and Closs, 2019), whereas headwater populations are stable with relatively low YoY densities (Huryn, 1996; Kristensen and Closs, 2008a; Kristensen and Closs, 2008b; Jones, Akbaripasand, Nakagawa and Closs, 2019). However, the fine-scale temporal dynamics of YoY brown trout in sites with diadromous and resident life histories remain unknown. Also, the role of environmental characteristics, spawning investment, and YoY's densities in the dynamics of migrations of diadromous and resident trout offspring are unknown. Therefore, the aim of this study was to investigate population dynamics at a fine scale, in order to better understand these important drivers of recruitment in diadromous and resident brown trout populations in New Zealand.

We studied an important spawning tributary of the Taieri River, New Zealand's fourth longest river, as a model system for evaluating the factors controlling fine-scale spatiotemporal population dynamics of YoY brown trout in reaches dominated by either spawning diadromous or resident fish. We predicted that longitudinal variation in the abundance of YoY trout along Silverstream would be primarily driven by the relative difference in parental spawning investment by diadromous and resident trout along the stream. These predictions are based on the data on spawning investment of brown trout we collected along the model stream, combined with published strong stock-recruitment correlation (Ricker, 1975) described for European brown trout (Elliott, 1994; Nicola and Almodovar, 2002; Sánchez-Hernández et al., 2016). Broad-scale patterns in the wider Taieri River catchment suggest that diadromous fish with high reproductive potential dominate lower altitudes, whereas resident fish with low reproductive potential dominate headwaters (Kristensen et al., 2011; Jones, Akbaripasand, Nakagawa and Closs, 2019). We also predicted that the primary factors driving YoY trout population dynamics will change from downstream to upstream — with intra-specific competition (biotic) driving population dynamics in downstream reaches, and environmental factors (abiotic) driving populations in the headwaters. This prediction is based on density-dependent population dynamics of juvenile salmonids observed at high densities (Keeley, 2003; Einum, Sundt-Hansen and Nislow, 2006; Landergren, 2004) and the potential of harsh environmental conditions to override the density-dependent population processes and maternal effects (Elliott, 1994; Richard, Cattaneo and Rubin, 2015; Syrjänen, Ruokonen, Ketola and Valkeajärvi, 2015). To test our predictions, we collected and assessed data on brown trout spawning investment, density and migration of the offspring, river discharge, temperature, and other environmental characteristics important for salmonids along Silverstream during 2016–2017. Thus, the focus of the study is to determine the key potential drivers of migrations of early life history of brown trout along the model stream, and therefore the recruitment of the population of the species inhabiting Taieri River catchment.

Materials and methods

Study area

To evaluate brown trout spawning investment and the spatiotemporal population dynamics of YoY fish, data was collected along the Silverstream, a 30-km long tributary of the Taieri River, which is the fourth longest New Zealand river, located in the south-eastern South Island. The Silverstream is one of the key spawning tributaries for diadromous brown trout from the main river channel and estuary of the Taieri River (Kristensen et al., 2008a). The spawning distribution of trout with a diadromous life history is limited to the lower and middle reaches of the stream (Kristensen et al., 2011). The upper part of the Silverstream is inaccessible to migratory trout due to a weir constructed in 1881 (Kristensen et al., 2011). The lower reaches of the stream are used for spawning by large migratory estuarine and potamodromous trout (Kristensen et al., 2011), generating high spring densities of juvenile fish which then decline sharply over the following 2-3 months (Kristensen and Closs, 2008a). Above the weir the population of resident fish is characterized by lower densities, a multicohort structure and a stable population of YoY trout (Kristensen and Closs, 2008b;

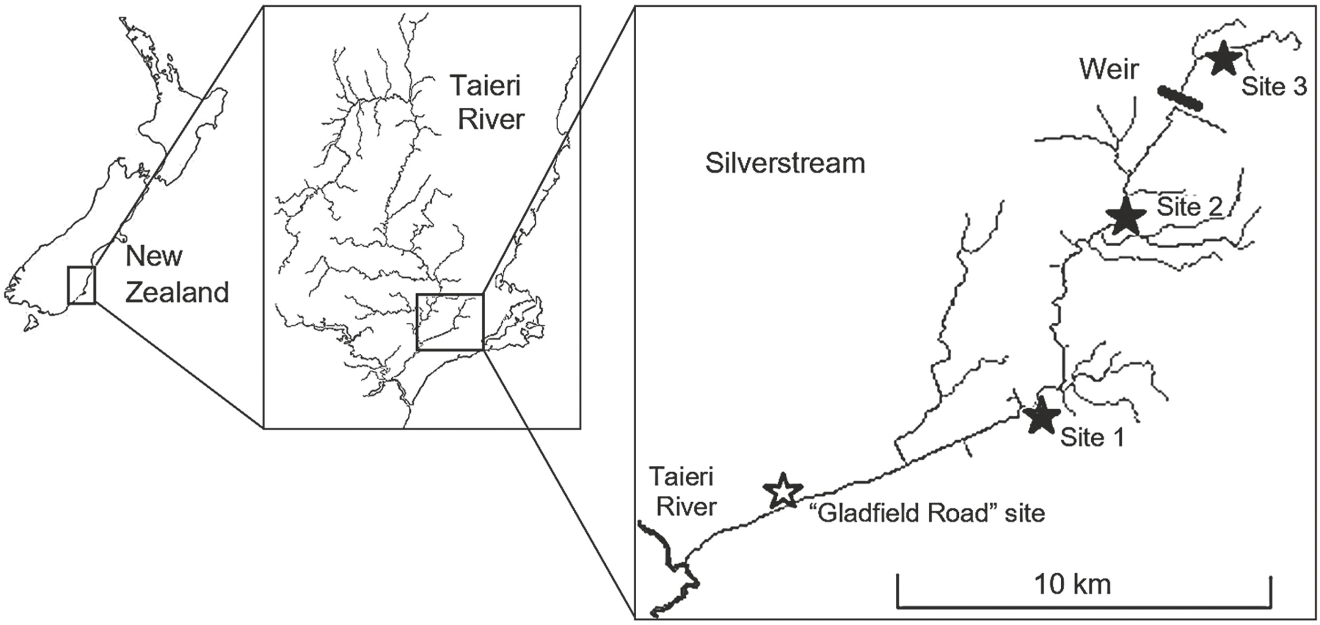

Fig. 1. Map indicating the position of the Taieri River catchment within New Zealand, as well as the model spawning tributary (Silverstream) and individual study sites Gladfield Road, 1, 2 and 3 with distance from stream mouth.

Jones, Akbaripasand, Nakagawa and Closs, 2019). The data on adult brown trout characteristics and parental spawning investment of both diadromous and residential life histories was collected along the stream from the confluence with the Taieri River to above the weir. The information on spatiotemporal dynamics of YoY trout were collected at four study sites (Fig. 1): Gladfield Road site located 2.8 km upstream from the confluence with the Taieri River; Site 1 located 10.2 km upstream from the confluence; Site 2 located 17.7 km upstream; and Site 3 located in the headwaters 25.1 km upstream from the confluence and upstream of the weir.

Fish data sampling

The extent of trout spawning in Silverstream downstream of the weir was assessed over four surveys completed between 11th–19th of June and five surveys between 2nd–22nd of July 2016. For each spawning survey, one 2–5-km-long stream section located between the confluence with the Taieri and the weir was surveyed. The position of each redd, and any dead or alive adult fish, were recorded using a GARMIN GPSmap 60CSx, with each fish photographed. To compare key traits of spawned Silverstream trout with ones from the native European range, the fork length of dead fish was measured to the nearest 1 mm. If the condition of the fish was suitable for necropsy, they were dissected for sex determination and an assessment of gonad condition. Females with full gonads that had died before spawning were used for fecundity calculations. The sagittal otoliths were extracted from all dead specimens for age estimates.

To evaluate the spawning investment of resident trout inhabiting the reach upstream of the weir, the density and biological characteristics of adult fish were assessed along a 470-m-long stream section on the following dates: 7 Nov. 2016; 16 Jan. 2017; 19 Feb. 2017; 19 Mar. 2017; 15 May 2017; 23 Aug. 2017 and 10 Oct. 2017. Fish were sampled by single-pass electrofishing using a Kainga EFM 300 backpack electro-fisher (NIWA Instrument Systems, Christchurch) with 200–600 V pulsed DC current. Density was estimated from the single-pass abundance data (Zippin, 1956; Kruse, Hubert and Rahel, 1998; Foley, Rosenberger and Mueter, 2015; Mikheev et al., 2020). Captured fish also had their fins clipped and released for mark-recapture estimates of abundance using the Chapman estimator method (Chapman, 1951). On the last sampling date (Oct. 2017), all captured fish were euthanised using AQUI-S®, immersed in ice, and transported back to the laboratory for detailed analysis of sex, fecundity, and other key reproductive and population parameters.

The densities of YoY fish were assessed monthly from October 2016 until April 2017 at four locations (Fig. 1). The Gladfield Road site was assessed only in October 2016. Study Sites 1, 2 and 3 were regularly observed until April 2017. The YoY trout abundance was assessed by spotlighting, given its low impact and high efficiency (Hickey and Closs, 2006). Each study site was divided into 30-m-long sections, three of which were chosen for spotlight surveys on any one night. Spotlighting commenced at least one hour after sunset, at baseflow conditions scanning with an LED headlamp from bank to bank working upstream. Juveniles were classified to YoY and ≥1+ cohort groups based on size (Lund, Olsen and Vøllestad, 2003). A sample of juveniles were also collected to confirm length/age estimated. Fish were euthanised by an overdose of AQUI-S® fish anaesthetic, preserved in 70 % ethanol, followed by length (± 0.1 mm) / weight (± 0.01 g) measurement, and sagittal otolith extraction.

To estimate the migration (both up and downstream) of YoY trout, fish movement was estimated at Sites 1, 2 and 3 using fry traps comprising two fyke nets oriented up and downstream, joined by a central wing (3-mm mesh) that blocked the stream and directed fish into the fykes. Assuming that diurnal feeding migrations (Hubert, Harris and Wesche, 1994; Bardonnet, Poncin and Roussel, 2006; Conallin et al., 2014) can affect the results of migration assessment, the traps were installed in the middle of the fastest riffle of each stream site. We assumed that such habitats with water velocity 0.7–0.9 m s^{-1} were not used as YoY trout feeding stations (Heggenes, Baglinière and Cunjak, 1999; Jowett and Richardson, 2008; Ayllón, Moran and Garcia-Vazquez, 2006), hence only individuals actively moving through the riffles would be captured. To protect captured fish from the high water velocity conditions, the downstream fyke was joined to a 25 x 100 cm box to provide a secure shelter. To prevent clogging, three debris fences with mesh size 25, 38 and 50 mm were deployed upstream of the trap. The traps were deployed at each sampling location once a month on the new moon from October till April for 24 hours. Traps were checked every 3 hours, and any fish were counted and released in the direction that they had been travelling when trapped.

Environmental data sampling

The physical habitat at Sites 1, 2 and 3 was assessed using published protocols (Jowett, Hayes and Duncan, 2008; Harding et al., 2009; Bouwes et al., 2011). All mesohabitats were classified into three basic groups — riffle, run and pool (Jowett, 1993). To standardise procedures, each stream segment was selected to include at least three pools. Key mesohabitat features measured included area, average and maximal depth, water velocity, the proportion of mesohabitat area with possible trout cover (wooden debris, macrophytes, overhanging vegetation and undercuts, cobbles and boulders), and the percentage of shaded area. Bed substrate composition was described following the Udden — Wentworth scale and evaluated visually as a proportion of bedrock, boulders (particles with size >256 mm), cobbles (64–256 mm), gravel (2–64 mm), sand and silt (<2 mm). Water velocity (m s^{-1}) was measured using a Marsh — McBirney 2000 Flo-Mate portable velocity meter. Water temperature at the sites was recorded using HOBO 64K-UA-002-64 data loggers. Stream discharge was estimated using data provided by Otago Regional Council based on the discharge gauge located downstream of Sites 1, 2 and 3 (Lat –45.87, Long 170.34). Discharge at the upstream sites was adjusted as a proportion of average area of riffles in the stream cross section at each site relative to the channel area at the discharge gauge. The areas of riffle cross sections used for conversion were: gauging site: 0.86 (±0.08 SE) m^2, Site 1: 0.76 (±0.10) m^2, Site 2: 0.67 (±0.11) m^2, and Site 3: 0.37 (±0.03) m^2.

To examine the relationship between water temperature and discharge on juvenile trout population dynamics, we used the environmental data collected during the period prior to each fish sampling event. Mean water temperature was used to predict fish loss rate considering the importance of thermal conditions on trout distribution and population dynamics (Aldven, Degerman and Hojesjo, 2015; Santiago et al., 2015). The median and maximum discharge values were used to estimate mean discharge and flood (maximum discharge) relationships with juvenile trout density (Table 1).

Table 1. The data used to estimate effects of water temperature and discharge on YoY trout loss rate

Site	Sampling period	Water temperature, °C*	Discharge, $m^3 s^{-1}$**
1	18/10–9/11	12.15 (2.02)	0.5 (3.08)
	9/11–9/12	12.19 (2.02)	0.5 (3.08)
	9/12–20/01	14.88 (2.42)	0.25 (2.01)
	20/01–24/02	14.74 (2.76)	0.34 (19.37)
	24/02–24/03	14.08 (2.19)	0.18 (1.24)
	24/03–28/04	11.49 (1.59)	0.41 (28.49)
2	25/10–10/11	9.76 (1.39)	0.31 (25.11)
	10/11–16/12	11 (1.27)	0.56 (13.16)
	16/12–21/01	11.67 (1.24)	0.21 (1.76)
	21/01–23/02	12.07 (1.61)	0.32 (17.07)
	23/02–22/03	11.42 (1.3)	0.17 (1.09)
	22/03–29/04	9.95 (0.96)	0.3 (25.11)
3	20/11–15/12	9.93 (1.51)	0.3 (1.85)
	15/12–16/01	11.23 (1.6)	0.11 (0.35)
	16/01–18/02	10.93 (1.44)	0.18 (9.43)
	18/02–18/03	11.32 (1.81)	0.1 (0.6)
	18/03–22/04	9.53 (1.14)	0.1 (13.87)

Notes: *The water temperature values presented as mean and SD (in brackets). ** The discharge presented as median and maximum values (in brackets).

To evaluate the spawning capacity of each site, we calculated the sum of the areas located at the end of pools and runs merging into riffles, which are the preferred spawning habitat for brown trout (Jonsson and Jonsson, 2011). Only zones with loose gravel and cobbles, flow velocity between 0.25–0.62 m/s and depth between 0.11–0.42 m were used, corresponding with spawning suitability curves for substrata composition, water velocity and depth in rivers with discharge <10 $m^3 s^{-1}$ (Zimmer and Power, 2006; Louhi, Mäki-Petäys and Erkinaro, 2008). For Site 3, only areas with suitable spawning gravel were counted due to the assumption that the median particle size of the suitable spawning substrate is near to 10 % of a spawner body length (Kondolf and Wolman, 1993).

Otolith preparation and analysis

Analysis of annual increments in sagittal otoliths was used to estimate the age structure of both diadromous and resident adult trout, and to sort trout into age cohorts where size distributions overlapped. The otoliths were cleaned of adhering tissue, air dried, mounted flat on glass microscope slides using thermoplastic resin (Crystalbond 509), and each side polished using fine-grit sandpaper (P1500 and P2000 grit) and lapping film (3–30 μm, 3M). Annual increments were counted using light microscopy (Olympus SZ2-ILST, Olympus Corp.) under 10-40X magnification.

Data analysis

To estimate the spawning investment of diadromous trout in Silverstream, the number of eggs deposited per unit area of stream bed was calculated, and adjusted for female size using the fork length / eggs per redd regression published by Elliott (1995): $\log_{10}E = \log_{10}(-2.203 \pm 0.332\ (95\,\%\ \mathrm{CI})) + (2.048 \pm 0.131\ (95\,\%\ \mathrm{CI}))\log_{10}L$, $R^2 = 0.97$, where E is eggs per redd and L is fork length in mm. We assumed each female spawned in a single redd (Elliott, 1995; Rubin, Glimsäter and Jarvi, 2005), allowing estimation of the arithmetic mean (±SE) of the number of deposited eggs per unit area.

To estimate the spawning potential of resident trout inhabiting the Silverstream headwaters (Site 3), the abundance of stream resident adults was calculated the abundance of stream resident adults was calculated using two methods: conversion of the single-pass abundance data to density by Zippin (1956) three-pass removal using linear regression, and by mark-recapture estimates applying the Chapman estimator method (Chapman, 1951). To convert single-pass abundance data to three-pass removal values, the following formula was applied: $TP = 1.775\ SP + 0.020$, $R^2 = 0.96$, where TP = density by Zippin's three-pass removal method (ind./m^2), and SP = single-pass density (ind./m^2). Fecundity was calculated using the equation developed by Jonsson and Jonsson (1999) for stream resident brown trout: $\ln F = 0.836 \ln W + 1.735$, $R^2 = 0.70$, where F = fecundity (eggs), and W = somatic weight (g). Then we assumed that each female deposited 85.5 % of their eggs into a redd (Elliott, 1995), and that all mature females in the population spawned within the 470-m long headwater study reach. The calculation of spawning investment of residential trout was based on May sampling data, which is the main spawning period for New Zealand brown trout (May–June). To assess the temporal stability of the resident fish population, a one-way ANOVA compared adult size collected at each sampling event across each month of sampling. At each sampling event, adult residents were collected (n = 14 to 23 fish per event), and each individual was used as a replicate.

To test the relationship between adult trout spawning investment and spring YoY density at the four sites, linear regressions were run using the lm function in R version 3.4.3 (R Core Team, 2017). To test the effect of spawning input on spring YoY density, the mean density of deposited eggs at locations used for YoY sampling was used as a predictor. The spring values of YoY fish density at each of three 30-m-long stream sections at each study site (Gladfield Road site, Sites 1, 2 and 3; with three replicates per site) were used as a response variable. The spawning input and fish density data were 4th root and $\log_{10}$ — transformed for normality, respectively. Residuals were plotted against predictors and a Q-Q plot was used to check the normality of residuals. Residuals *versus* leverage plots, with calculation of Cook's distance, were used for identification of the influential outliers in a set of predictor variables. For this study, a confidence level of 95 % ($\alpha = 0.05$) was used.

To estimate changes in the abundance of juvenile brown trout by site, the daily instantaneous loss rates were calculated using the formula: $LR = (D_0 - D_t)/t$, where LR is loss rate (ind.*100 m^{-2} *day^{-1}), D_0 is the initial fish density (ind.*100 m^{-2}), D_t is the final density (ind.*100 m^{-2}) and t is the period between sampling in days. A two-way ANOVA was applied for the estimation of the effect of spatial (site) and temporal (month of sampling) categories and their interactions (site * month) on the dynamics of YoY loss rate and density. The monthly data on YoY fish density and loss rate were used as a response variable for each site. At each site, data collected at three monitored stream sections were used as replicates. The data on instantaneous daily loss rate and month of sampling was 4th root-transformed, and density values were $\log_{10}$-transformed for normality. Mesohabitat environmental characteristics were excluded from the analysis of the effect of key environmental factors controlling density and loss rate of YoY fish, given their temporal consistency. As such, we used the sampling location, assuming it took mesohabitat variables into account, as a proxy for testing the effect of the environmental variables on YoY density and instantaneous daily loss rate.

To test for the predicted relationships between biotic and abiotic factors, and the population dynamics of YoY trout along the stream and across seasons, multiple linear regressions were applied using the lm function in R. The data collected at each of the three 30-m-long monitored stream sections per site were pooled and used as a replicate for each sampling event. The YoY loss rate for each monitored stream section was used as the response variable. Juvenile trout density and the migration rate measured at the start date of the period used for loss rate calculations were set as predictors. The water flow and temperature data collected during the period between samplings were also used as predictor variables (Table 1). Multiple linear regressions were also used to test the effect of stream discharge and temperature on YoY emigration from Silverstream. In this case the combined downward migration data from sites 1 and 2 were chosen as a response variable and the data on water temperature (°C) and stream discharge collected at the time of YoY trout migrations assessment were used as a predictor. The data were checked for normality prior to the analysis and ln, $\log_{10}$ or 4^{th} root transformed if necessary. For testing the collinearity of the variables used in linear regression analysis, the variance inflation factor (VIF) was applied using the VIF package in R. Following standard protocols, all variables with VIF values exceeding 10 were removed (James et al., 2014). The best fitting model was then identified using stepwise AIC with the step function in R. Model selection was based on a backwards stepwise procedure, starting with the saturated model, then removing predictors one by one until the AIC stopped improving.

To differentiate the sampling locations by the environmental characteristics most important for brown trout, a one-way ANOVA with Tukey HSD test for multiple comparison was applied. The environmental variation within and across sampling locations was assessed using a separate analysis for each environmental characteristic for each of the three major habitat types — riffles, runs and pools. The measurements of each environmental characteristic across the different habitats were used as the response variables, and site — as a categorical variable. The number of riffles, runs and pools observed at each of the study sites were used as a replicate for observed environmental characteristics. At sampling sites 1, 2 and 3, the number of major habitats (replicates) were as follows: riffles — 23, 14 and 8; runs — 23, 20 and 11; pools — 7, 13 and 3. For subsequent ANOVA analysis, the data were checked for normality and ln, $\log_{10}$ or 4^{th} root transformed if necessary prior to the analysis. Homogeneity of variances were tested using Levene's test. Eta-squared values were computed to measure the strength of the relationship between analysed variables. The aov, etasq, leveneTest and TukeyHSD functions in R version 3.4.3 (R Core Team, 2017) were applied.

Results

Environmental conditions by site

Silverstream Sites 1, 2 and 3 differed from each other in terms of proportions of major habitat types (Table 2). Runs were the dominant mesohabitat along all three reaches, with the highest proportion along Site 1 (downstream). The proportion of riffle was highest along the headwater reach (Site 3), whereas pools represented almost a third of the mesohabitat along Site 2.

The proportion of boulders was highest at Site 2, confirmed by *post hoc* comparisons using the Tukey HSD test (ANOVA outputs for riffles $F_{2,42} = 5.5$, $p = 0.01$; for runs $F_{2,51} = 16.1$, $p < 0.01$). Gravel dominated pools along the lower reaches ($F_{2,20} = 4.3$, $p = 0.03$), whereas sand was the most abundant along the headwater reach (ANOVA for riffles $F_{2,42} = 10.3$, $p < 0.01$; for runs $F_{2,51} = 6.7$, $p < 0.01$). The distribution of the shelters among the observed stream sections was lowest at Site 1 (ANOVA for pools $F_{2,20} = 5.1$, $p = 0.04$). Tree canopy was the

Table 2. Physical characteristics of basic mesohabitats of study Sites 1, 2 and 3

Site[1]	Habitat type	Percentage of total area of meso-habitats, %	Depth average, cm	Water velocity (m/s)	Bottom substrate granulometric composition, %					Proportion of the area with shelters, %	Proportion of unshaded water surface, %
					Bed-rock	Boulders	Cobbles	Gravel	Sand and silt		
1	pool	7.9	68±18[2]	0.19±0.1		10.0±0.0	24.0±7.5	64.0±5.1	16.7±5.2	37.8±6.0	60.0±10.5
	riffle	19.5	19±1.8	0.75±0.1	5.0±0.1	18.9±3.0	48.8±5.5	42.6±6.3	6.0±0.5	63.9±6.7	63.9±4.3
	run	70.5	31±2.9	0.27±0.1		14.4±2.7	43.8±5.1	50.4±4.9	9.0±0.6	60.4±5.4	61.5±4.0
2	pool	29.9	103±9.2	0.04±0.0	1.5±0.3	27.1±6.4	15.0±3.2	39.3±6.2	15.0±2.5	68.6±11	40.7±9.5
	riffle	19.1	18±2.9	0.65±0.1		28.2±7.0	36.5±5.5	45.8±7.6	6.7±0.8	77.8±7.6	41.1±5.5
	run	48.5	30±2.2	0.24±0.0	1±0.0	24.4±3.7	29.2±3.9	44.7±4.3	10.9±0.7	66.2±6.1	43.0±5.0
3	pool	14.7	57±6.8	0.13±0.1	7.5±0.2	18.3±8.5	30.0±8.9	21.7±3.4	25.0±6.7	62.1±18	50.0±4.5
	riffle	39.6	14±0.8	0.7±0.1	3±0.0	12.5±2.0	45.0±5.3	30.6±3.1	9.3±2.3	73.1±6.7	65.0±7.6
	run	45.7	26±2.0	0.28±0.0	5±0.0	11.4±1.7	39.1±4.7	32.3±4.5	16.8±2.6	71.2±5.0	63.6±5.3

Notes: [1] The total lengths of the observed stream segments are 910, 599 and 163 m for sites 1, 2 and 3 respectively. [2] The physical characteristics are presented as mean ± SE.

most developed at Site 2. This part of the stream was also characterised by the highest water surface shading (ANOVA for riffles $F_{2,42} = 6.1$, $p < 0.01$; for runs $F_{2,51} = 5.8$, $p < 0.01$).

Spawning investment and adults' traits

In total, 77 redds of diadromous trout were identified between the confluence with the Taieri River and the weir. Only 1 redd was detected along the first 5 km stream segment, and only 3 redds were identified along the most upstream 3 km reach to the weir. In contrast, 22 redds were counted between 8–11 km from the stream mouth (Table 3).

In total, 71 live and 28 dead adult trout were counted along Silverstream from the Taieri confluence to the weir at the time of spawning surveys. Most of the live fish were detected on the first two trips (11 and 14 June 2016) near redds and resting in pools. The redds were typically located in likely downwelling flow zones located at the downstream end of runs. Up to five brown trout carcasses were encountered on each survey. Of the dead fish, 15 were females and 11 males. Twelve dead females were dissected with five having full gonads. The fecundity of two females was evaluated: 3037 eggs were counted in a 496 mm long female (age 5+) and 2459 eggs in a 435 mm long female (age 4+). The males were also dissected but spawning condition could not be determined. A third of the dead fish were in a fresh condition, without any obvious injuries and otherwise appeared healthy. The size of the females ranged between 333–527 mm (mean 457 ± 13.3 SE) and males between 368 and 647 mm (mean 459 ± 20.8 SE). The age was determined for all collected trout carcasses, and varied between 3+ and 5+ years, with 4+ and 3+ fish being the dominant year class in females and males, respectively. Six of 15 females were spawning at age 3+ and one fish was 5+. Only 3 spawning males were 4+, with the rest at 3+ years.

Table 3. Density of brown trout redds and the average number of deposited eggs (±SE) per stream area at different sections of the Silverstream

Stream section (distance from stream mouth)	Redds/ha	Thousands of eggs / ha
1 (0–5 km), Gladfield Road site	0.5	0.8±0.04
2 (6–7 km)	10.9	19.2±0.97
3 (8–9 km)	14.8	26.2±1.31
4 (10–11 km), Site 1	13.9	24.5±1.23
5 (12–14 km)	8.2	14.5±0.73
6 (15–17 km)	6.5	11.5±0.58
7 (18–20 km), Site 2	4.9	8.7±0.43
8 (21–23 km)	2.9	5.2±0.26
9 (24–24.5 km), Site 3*	131.4**	15. 4±0.9

* — habitats of stream residential brown trout; ** — spawning females per stream area unit.

The average number of eggs deposited per redd by diadromous fish was estimated at 1768.2±88.8 SE. The highest density of eggs per stream area unit was evaluated for the sections 3 and 4 which includes Site 1. At Site 2, density of eggs was at least two-fold lower (Table 3).

The number of adult resident fish along Site 3 was low and only varied slightly over the year. Adult trout abundance was the lowest (24 fish) in Aug., the highest (51 fish) in Jan, and the average for all sampling events was equal to 41 (± 14.4 SE) fish. The average recapture rate was 42.1 ± 3.4 SE % with the lowest (35 %) in Feb. and highest (53.8 %) in Aug. Fish abundance evaluated by the Chapman estimator was close to the modelled regression line. The lowest number of adult stream residents was estimated in October (28 fish), the highest in March (50 fish) with an average of 40 (±4.3 SE) individuals.

Mature residents at Site 3 were characterised by small size, although their age composition and spawning investment was similar to that of diadromous trout spawning below the weir. The size of adult resident females varied between 142 and 228 mm (mean 187 ± 7.7 SE), and males between 113.5 and 225 mm (mean 192 ± 11.0 SE). The age ranged from 2+ to 5+ for 13 dissected mature females (three 2+ fish; one — 4+; two — 5+; and six — 3+), and from 1+ to 5+ for 9 males (one individual 1+; four — 3+; three — 5+; one — 5+). At Site 3, during the spawning season in May, the number of adult fish was estimated at 35 individuals. Based on a sex ratio of 1.4 female: 1 male derived from dissected specimens, we estimate that approximately 21 of these individuals were females. Assuming all females spawned, the density of eggs was estimated at 15,361 ± 919 SE (range 7,782–23,866) eggs per ha of the headwater stream reach (Table 3).

Stream spawning capacity

The total area of habitat suitable for trout spawning was estimated to be 1335 m^2 at Site 1 (23.9 % of total area of the observed stream segment), 871 m^2 at Site 2 (20.4 % of total area of the observed stream segment) and 52.2 m^2 at Site 3 (10.4 % of total area of the observed stream segment). Extrapolating the data on redd density (Table 3) to the area of available habitat suitable for trout spawning, the number of redds (or spawning females) for Sites 1, 2 and 3 was estimated as 8, 3 and 7 correspondingly. An area of habitat suitable for trout spawning and available for each spawning female spawn was estimated at 166.9, 290.3 and 7.5 m^2 respectively for Sites 1, 2 and 3.

Table 4. The seasonal change of brown trout YoY density (ind. 100 m^{-2}) and daily instantaneous loss rate (LR, ind. 100 m^{-2} day^{-1}) at three locations of the Silverstream

	Site	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Density	1	102.9±21.68	77.3±23.95	42.4±6.38	14.0±4.39	6.9±0.59	3.6±1.56	0.7±0.01
	2	35.6±20.23	82.9±25.23	47.1±21.10	24.2±4.90	50.4±16.04	16.2±2.47	5.6±1.35
	3		0.26±0.02	1.45±1.16	1.61±1.25	1.03±0.39	1.20±0.21	1.66±0.04
Loss rate	1		2.83±3.09	1.16±0.83	0.58±0.14	0.25±0.07	0.12±0.08	0.10±0.05
	2		–2.96±0.32	0.99±0.17	0.63±0.69	–0.78±0.50	1.27±0.52	0.28±0.05
	3			–0.48±0.26*	–0.05±0.02*	0.18±0.15*	–0.06±0.04*	–0.13±0.04*

Notes: the density (loss rate) is presented as an average ± SE; * the values of loss rate at Site 3 are close to zero and multiplied to 1,000.

Table 5. The diurnal dynamics of migrations (ind. per trap check), water temperature and stream discharge at three locations of the Silverstream

Time	Site	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
15:00 — 18:00	1					(1)		
	2			(1)				
18:00 — 21:00	1		1					
	2		1		(1)	2		
21:00 — 0:00	1		1	(1)	1			
	2		4	5 (1)	80 (6)	2 (1)	1	
0:00 — 3:00	1	91	5	(1)	5 (2)			
	2		1	2	16 (10)	1		1
3:00 — 6:00	1		1	1 (2)	3			
	2	8	1 (2)	2 (2)	23 (3)	1	(1)	
6:00 — 9:00	1	19			7			
	2	2	1 (2)		1	2	1	
9:00 — 12:00	1	1	(1)	(1)			(1)	
	2		1 (2)			3 (1)		
12:00 — 15:00	3			1				
	2				4			
Total in 24 hours	1	111 (0)	8 (1)	1 (4)	16 (2)	0 (1)	0 (1)	0 (0)
	2	10 (0)	9 (6)	9 (6)	124 (20)	11 (2)	2 (1)	1 (0)
	3		0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)
t, °C	1	9.9	11.7	16.7	12.5	16.7	13.1	10.2
	2	8.6	9.7	11.9	10.2	14.2	10.6	8.9
Discharge, m^3 s^{-1}	1	0.51	0.36	0.46	1.27	0.19	0.15	0.21
	2	0.35	0.28	0.24	0.37	0.19	0.14	0.16

Notes: diurnal dynamics of YoY's migrations presented as number of individuals captured by trap with fish moving down (and upstream). The data on water temperature and stream discharge used for linear regression model are presented as mean values calculated from hourly data collected at the time of YoY trout migrations assessment.

Abundance, population dynamics and movement of YoY brown trout

The first YoY brown trout were detected in the lower reach of the Silverstream at the start of October 2016 at the Gladfield Road site located near the Silverstream — Taieri River confluence, with an average density of 17.7 (±3.1 SE; range 11–26) fish per 100 m^2. The highest density of YoY trout across the sites was recorded at Site 1 in October, which was three-times higher than at Site 2. In the Silverstream headwaters, the first juvenile fish were detected in November at extremely low densities (Table 4). ANOVA outputs confirmed the upstream (outputs for site: $F_{1,51} = 58.40$, $p = < .001$) and seasonal (outputs for month: $F_{1,51} = 9.30$, $p =$ YoY fish abundance .032) reduction of YoY density, showing that YoY fish abundance varied with respect to site and month.

At Site 1, the density of YoY fish constantly declined over the study, with the highest instantaneous daily loss rate during spring/summer. By April, the density of YoY trout at Site 1 was close to zero. At Site 2, the density of juvenile fish was lower than that at Site 1 in spring, but higher in the summer. The seasonal change of juvenile trout abundance at Site 2 had a negative trend, but decreased in a two-step pattern, with peaks in November and February. The YoY loss rate at Site 2 was higher in the second half of the season in comparison to earlier in the season. At Site 3 the density of YoY trout increased in December and was relatively stable over subsequent months (Table 4). Site was a significant predictor for loss rate by itself ($F_{1,41} = 4.40$, $p = .042$) but also in combination with date ($F_{1,41} = 9.89$, $p = .003$) confirming a general upstream reduction of YoY loss rate over time. However, month was not related to loss rate for data combined from the three sites ($F_{1,41} = 0.50$, $p = .483$). Results were significant for the separate datasets of Sites 1 and 2, but not for Site 3. The strong effect of sampling month confirmed seasonal reduction of loss rate for Site 1 ($F_{1,16} = 23.54$, $p = < .001$), and a positive seasonal trend of loss rate at Site 2 ($F_{1,16} = 4.99$, $p = .043$).

Movement of YoY trout occurred in both up and downstream directions, although the majority were captured moving downstream and at night (Table 5). Downstream migration peaked in October at Site 1, and in January at Site 2. No fish were trapped at Site 3, except for one individual moving downstream in December. At the downstream sites, individuals moving upstream were captured every month from November until March, with the peak occurring in January at Site 2. Downstream movements generally occurred in the first half of the night, whereas upstream movement occurred in the second half of the night or during the morning.

Factors driving recruitment of brown trout

The number of deposited eggs per unit area was a poor predictor of spring values of YoY trout density at all sites ($F_{1,10} = 0.08$, $t = 0.286$, $p = .780$, $R^2 = .012$) (Fig. 2).

Fish density and migration rate were significant positive predictors for YoY loss rate at Site 1, whereas none of the measured categorical variables were related to YoY loss rate at Sites 2 or 3. Water temperature and flow were excluded from the best fitting linear model for Site 1. The analysis did not reveal any significant predictors of YoY trout loss rate at Site 2 even if the final model included density as the only predictor, though the

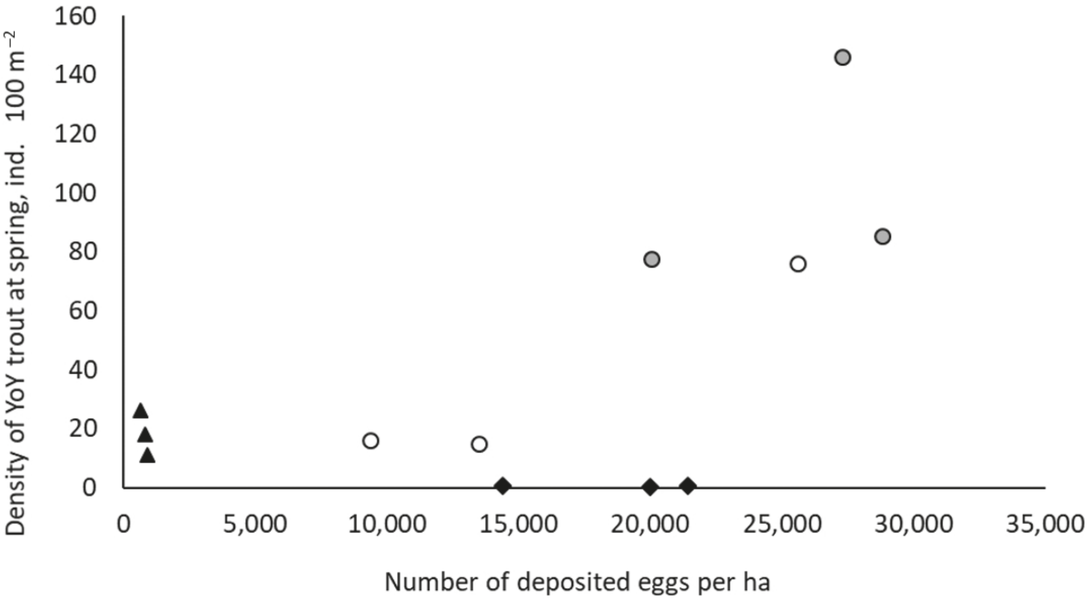

Fig. 2. Density of YoY trout in spring in relation to number of deposited eggs for Gladfield Road site (black triangles), Site 1 (grey circles), Site 2 (white circles) and Site 3 (black diamonds).

Table 6. Multiple linear regression analysis testing the relationships between biotic (density and migration rate) and abiotic (water temperature and flow) predictors of seasonal dynamics of YoY trout instantaneous daily loss rate at three sampling locations of Silverstream at season 2016–2017

Effect	Site 1			Site 2			Site 3		
	Estimate ± SE	t	p	Estimate ± SE	t	p	Estimate ± SE	t	p
(Intercept)	0.05±0.105	0.49	0.63	–0.60±0.44	–1.35	0.19			
Density	**0.21±0.082**	**2.58**	**0.02**	0.54±0.287	1.90	0.08	–0.01±0.004	–2.03	0.08
Migration rate	0.01±0.001	8.68	<0.01						
Temperature mean							0.01±0.004	2.00	0.08
Maximal discharge							0.0003±0.0002	1.60	0.15

Notes: effect of the significant predictors in bold.

p value was close to significance. The best fitting model used for the evaluation of the effect of the measured parameters on juvenile trout loss rate at Silverstream headwaters included only two abiotic factors — mean water temperature and maximum discharge, but was not significant (Table 6).

The migrations were not associated with water temperature ($F_{1,13}$= 0.90, t = –0.98, p = .359, R^2 = .03) or stream flow ($F_{1,13}$ = 1.15, t = 1.28, p = .239, R^2 = .02) despite some evidence of discharge affecting YoY trout migrations in the raw data. The statistical outputs of the analyses did not show significant associations, likely because of the January data, when sampling occurred under high flow conditions. At this sampling, the second peak of emigrating YoY trout was evaluated at Site 1 and the seasonal maximum of both up and downstream migrations was assessed at Site 2 (Table 4).

Discussion

Brown trout spawning investment and young-of-the-year abundance

The overall finding was that the number of deposited eggs per unit area was a poor predictor of spring values of YoY trout density. This did not align with the expectation that parental investment would influence YoY trout density in spring (Elliott, 1994), and may be associated with the weak relationship between the densities of both eggs and juvenile fish across sampling sites. Strong associations between parental spawning investment and offspring abundance have been described for trout with both diadromous and residential life histories in Europe (Nicola and Almodovar, 2002; Sánchez-Hernández et al., 2016). This relationship may hold true for Sites 1 and 2 where juvenile trout density corresponded to adult reproductive input. These sites are intensively used by diadromous adults for reproduction, and so we suspect that spawning conditions are close to optimal at this area. The converse pattern was observed close to the confluence at the Gladfield Road site and in the headwaters. Only one redd was detected at the Gladfield Road site, and the first YoY trout were detected upstream of this redd. These YoY individuals must have originated from the redds located further upstream, and dispersed downstream soon after emergence (Elliott, 1986; Hayes, 1988; Landergren, 2004; Boel et al., 2014). In the stream headwaters, a relatively high spawning investment by stream resident trout contrasts with the low density of juveniles, perhaps due to reduced spawning efficiency of adults and/or high mortality during the early development stages. The headwater reaches of Silverstream are periodically subjected to a high fine sediment load due to landslips, which can significantly reduce egg survival during the early embryogenesis period (see Conallin, 2004; Cocchiglia et al., 2012).

In comparison to European studies (Elliott, 1985, 1987), the spawning investment and spawning efficiency of brown trout in Silverstream was relatively low, likely associated with low abundance and high mortality of adults. Low abundance would contribute to a relatively low number of deposited eggs: the average abundance of deposited eggs in Silverstream was equal to 13,828±744 SE eggs per ha for diadromous populations, and 15,361± 919 SE eggs per ha for stream residents. This is markedly less than observed in some English streams, where Elliott (1985, 1987) recorded mean values of eggs density of 704,800±105,300SE eggs per ha along migratory trout spawning reaches, and 42,300±4,600 SE eggs per ha for resident trout spawning reaches. The density of spawning females in Silverstream was equal to 18.3 ind./ha for Site 1, 7.4 ind./ha for Site 2 and 131.4 ind./ha for Site 3, which is lower compared to the density of migratory (762±86.8 SE) and resident (215±23SE ind./ha) spawning female trout in England (Elliott, 1985, 1987, 1994). Other factors negatively affecting the reproductive input include the observed pre-spawning mortality, which has not been previously described for this iteroparous species (Elliott, 1994; Jonsson and Jonsson, 2011; Lobón-Cerviá and Sanz, 2017). Assuming that the number of redds represents the number of spawning females, then the observed pre-spawning mortality rate represented 21% of the Silverstream spawning stock. One third of the dead fish had died before spawning. The reduced egg density cannot be explained by biological traits of Silverstream spawners. The size, sex ratio, age structure and fecundity of adults were close to those published for both migratory and resident forms of the species in Europe (Elliott, 1994; Nicola and Almòdovar, 2002; Acolas, Roussel and Baglinière, 2008). Deficiencies in the spawning capacity can also be excluded as a factor affecting trout reproductive input. Given the area required for one female to spawn (Ottaway, Carling, Clarke and Reader, 1981; Crisp and Carling, 1989), the extended reproductive period (Gortázar et al., 2007) and exploitation of spawning grounds by multiple adults (Gortázar, Alonso and García de Jalón, 2012), we can assume the spawning capacity of Silverstream is significantly underexploited by brown trout.

Endogenous and environmental factors in YoY trout population dynamics

YoY trout density and migration significantly affected its loss rate at lowland Site 1, but not at Sites 2 and 3. This supports our predictions, and may be driven by differences in competition associated with environmental variability between study sites (Elliott, 2006). Previous works (Kristensen and Closs, 2008a, 2008b; Jones, Akbaripasand, Nakagawa and Closs, 2019) and our data show evidence of upstream parallel reduction of spring density and self-thinning rate of YoY trout. Environmental differences between study sites could contribute to this pattern — the lower part of the Silverstream (Site 1) is characterised by little shading, more variable and higher daily mean water temperatures, and a lack of shelter for juvenile brown trout. Site 2 is characterized by high abundance of shelter in complex substrates, relatively more stable water temperatures, and extensive shading, suggesting highly suitable habitat for YoY trout (see Conallin et al., 2014). These differences could affect the carrying capacity and level of competition along each reach (Enefalk and Bergman, 2016) and high sensitivity of YoY trout to thermal conditions (Ayllón et al., 2013; O'Briain, Coghlan, Shephard and Kelly, 2019). Warm water temperatures increase the energetic demands of fish, and energetic constraints occur at a population level when food supply is unable to meet these demands, potentially leading to the population self-thinning phenomena (Jenkins, Diehl, Kratz and Cooper, 1999; Keeley, 2003; Lobón-Cerviá, 2008; Hayes, Olsen and Hay, 2010). This might explain the highest spring values of fish loss rate at Site 1 and the positive seasonal dynamic of YoY trout loss rate at Site 2, suggesting possible "bottleneck" conditions in spring for Site 1 and in summer/autumn for Site 2. At Site 3, low values of YoY density in combination with extensive habitat suitable for juvenile trout suggests a low level of intra-cohort competition at all times.

The high loss rate of diadromous offspring at lowland sites and the low stable density of stream resident offspring in the headwaters observed in this study is consistent with previous work, and suggests that density-dependent regulation of trout populations interacts with mesohabitat suitability and landscape context. Elliott (1987) argued optimal conditions, and ready-access for migratory trout, resulted in high population densities downstream reaches, leading to intra-specific competition and density-dependent population regulation. In contrast, in headwater reaches populated by resident trout, harsh conditions limited trout abundance, and little if any competition meant density-independent population regulation tends to prevail (Elliott, 1987). Analogous conclusions were reached by Vøllestad and Olsen (2008) who studied Norwegian brown trout, and Velez-Espino, McLaughlin and Robillard (2013) who worked with North American brook trout (*Salvelinus fontinalis*).

The importance of discharge on migrations, and thus population dynamics and recruitment of brown trout of the Taieri River, was evident in the January movement data. The January data were collected in high flow conditions following a moderate flood that coincided with the new moon (see also Hayes, 1988; Jowett and Richardson, 1989; Hayes, 1995; Slavík et al., 2012). In total, 124 YoY fish moving downstream were captured within 24 h at Site 2 at flow conditions 312–534 L s^{-1}. Eighty of these individuals were captured between 9 PM and midnight at flows of 436–463 L s^{-1} (more than double the median flow). To compare changes in migration intensity relative to discharge, the trap was deployed again the next day from 9 PM to 12 AM when flows were greatly reduced (298–291 L s^{-1}). Only 17 juveniles moving downstream were captured. The results from Site 2 are consistent with the results from the January sampling completed at Site 1 under high flow. In total 16 YoY trout emigrants were detected within 24 hours under flow 834–1751 L s^{-1}, which was the highest observed migration rate after the spring. Clearly, periodic installation of fry traps to estimate migration data carries with it the risk of obtaining 'snap-shots' of information influenced by immediate environmental conditions. The use of PIT tagging or Wolf trapping (Wolf, 1951) may be a preferable method allowing the continuous collection of data on movement and mortality, but in both cases the loss of information and equipment during flood events is likely (Holmes at al., 2014; Aarestrup, Birnie-Gauvin and Larsen, 2018).

Our results demonstrate strong spatial variation in the seasonal population dynamics of YoY brown trout abundance in the studied spawning tributary of Taieri River, and the factors likely driving those dynamics, and thus recruitment of the species, in the catchment. The densities of deposited eggs and juvenile fish were related at sites intensively used by diadromous adults for reproduction, but unrelated further upstream where resident trout spawned. Overall, there was no evidence of an overall relationship between initial spawning investment and subsequent YoY trout abundance. Density and migration were related to YoY brown trout loss rate along downstream reaches, where diadromous fish spawned. This result is consistent with previous studies (Elliott, 1987; Vøllestad and Olsen, 2008; Velez-Espino, McLaughlin and Robillard, 2013) indicating a shift from density-dependence to density-independence of YoY trout population dynamics moving upstream into reaches inaccessible to large migratory trout. Stream discharge was positively related to increased downstream migration of YoY trout (see also Jowett and Richardson, 1989; Hayes, 1995; Holmes at al., 2014; Bergerot and Cattanéo, 2017; Aarestrup, Birnie-Gauvin and Larsen, 2018).

Acknowledgements

The authors thank Jason Augspurger, Fasil Taddese, Sichen (Jeremy) Xu, Kim Garrett, Dylan Glaser and Julien Breda for their fieldwork assistance and Nicky McHugh for her help in the laboratory. Special thanks to Ryan Easton for help in writing. We thank two anonymous reviewers for their valuable comments and suggestions which significantly helped in the improvement of the text.

References

Acolas, M. L., Roussel, J. M., and Baglinière, J. L. 2008. Linking migratory patterns and diet to reproductive traits in female brown trout (*Salmo trutta* L.) by means of stable isotope analysis on ova. *Ecology of Freshwater Fish* 17:382–393. https://doi.org/10.1111/j.1600-0633.2007.00290.x

Aarestrup, K., Birnie-Gauvin, K., and Larsen, M. H. 2018. Another paradigm lost? Autumn downstream migration of juvenile brown trout: Evidence for a presmolt migration. *Ecology of Freshwater Fish* 27:513–516. https://doi.org/10.1111/eff.12335

Aldven, D., Degerman, E., and Hojesjo, J. 2015. Environmental cues and downstream migration of anadromous brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts. *Boreal Environment Research* 20:1–10.

Allen, K. R. 1951. The Horokiwi Stream — a study of a trout population. N. Z. Marine Dept., Fisheries Bulletin 10, 230 pp.

Ayllón, F., Moran, P., and Garcia-Vazquez, E. 2006. Maintenance of a small anadromous subpopulation of brown trout (*Salmo trutta* L.) by straying. *Freshwater Biology* 51:351–358. https://doi.org/10.1111/j.1365-2427.2005.01486.x

Ayllón, D., Nicola, G. G., Elvira, B., Parra, I., and Almodóvar, A. 2013. Thermal carrying capacity for a thermally-sensitive species at the warmest edge of its range. *PLoS ONE* 8(11):e81354. https://doi.org/10.1371/journal.pone.0081354

Bardonnet, A., Poncin, P., and Roussel, J. M. 2006. Brown trout fry move inshore at night: a choice of water depth or velocity? *Ecology of Freshwater Fish* 15:309–314. https://doi.org/10.1111/j.1600-0633.2006.00160.x

Bergerot, B. and Cattanéo, F. 2017. Hydrological drivers of brown trout population dynamics in France. *Ecohydrology* 10(1):e1765. https://doi.org/10.1002/eco.1765

Bjørnstad, O. N. and Grenfell, B. T. 2001. Noisy clockwork: time series analysis of population fluctuations in animals. *Science* 293:638–643. https://doi.org/10.1126/science.1062226

Boel, M., Aarestrup, K., Baktoft, H., Larsen, T., Madsen, S., Malte, H., Skov, C., Svendsen, J., and Koed, A. 2014. The physiological basis of the migration continuum in brown trout (*Salmo trutta*). *Physiological and Biochemical Zoology* 87:334–345. https://doi.org/10.1086/674869

Bouwes, N., Moberg, J., Weber, N., Bouwes, B., Bennett, S., Beasley, C., Jordan, C. E., Nelle, P., Polino, M., Rentmeester, S., Semmens, B., Volk, C., Ward, M. B., and White, J. 2011. Scientific protocol for salmonid habitat surveys within the Columbia Habitat Monitoring Program. Terraqua, Inc., Wauconda, WA.

Burnet, A. M. R. 1959. Some observations on natural fluctuations of trout population numbers. *New Zealand Journal of Science* 2:410–421.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. *University of California Publications in Statistics* 1(7):131–160.

Cocchiglia, L., Curran, S., Hannigan, E., Purcell, P. J., and Kelly-Quinn, M. 2012. Evaluation of the effects of fine sediment inputs from stream culverts on brown trout egg survival through field and laboratory assessments. *Inland Waters* 2(1):47-58. https://doi.org/10.5268/IW-2.1.495

Conallin, J. 2004. The negative impacts of sedimentation on brown trout (*Salmo trutta*) natural recruitment, and the management of Danish streams. *Journal of Transdisciplinary Environmental Studies* 32:1–12.

Conallin, J., Boegh, E., Olsen, M., Pedersen, S., Dunbar, M. J., and Jensen, J. K. 2014. Daytime habitat selection for juvenile parr brown trout (*Salmo trutta*) in small lowland streams. *Knowledge and Management of Aquatic Ecosystems* 413:09. https://doi.org/10.1051/kmae/2014006

Crisp, D. T. and Carling, P. A. 1989. Observations on siting dimensions and structure of salmonid redds. *Journal of Fish Biology* 34:119–134. https://doi.org/10.1111/j.1095-8649.1989.tb02962.x

Dahlgren, J., Bengtsson, K., and Ehrlén, J. 2016. The demography of climate-driven and density-regulated population dynamics in a perennial plant. *Ecology* 97(4):899–907. https://doi.org/10.1890/15-0804.1

Dennis, B. and Traper, M. L. 1994. Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs* 64:205–224. https://doi.org/10.2307/2937041

Einum, S., Sundt-Hansen, L., and Nislow, K. H. 2006. The partitioning of density dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* 113:489–496. https://doi.org/10.1111/j.2006.0030-1299.14806.x

Elliott, J. M. 1985. Population regulation for different life-stages of migratory trout *Salmo trutta* in a Lake District Stream, 1966-83. *Journal of Animal Ecology* 542:617–638. https://doi.org/10.2307/4503

Elliott, J. M. 1986. Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a Lake District stream. *Journal of Animal Ecology* 55:907–902. https://doi.org/10.2307/4424

Elliott, J. M. 1987. Population regulation in contrasting populations of trout *Salmo trutta* in two Lake District streams. *Journal of Animal Ecology* 56:83–98. https://doi.org/10.2307/4801

Elliott, J. M. 1994. Quantitative ecology and the brown trout. Oxford Series in Ecology and Evolution. Oxford UK, Oxford University Press.

Elliott, J. M. 1995. Fecundity and egg density in the redd for sea trout. *Journal of Fish Biology* 47:893–901. https://doi.org/10.1111/j.1095-8649.1995.tb06010.x

Elliott, J. M. 2006. Periodic habitat loss alters the competitive coexistence between brown trout and bullheads in a small stream over 34 years. *Journal of Animal Ecology* 75:54–63. https://doi.org/10.1111/j.1365-2656.2005.01022.x

Enefalk, Å. and Bergman, E. 2016. Effect of fine wood on juvenile brown trout behaviour in experimental stream channels. *Ecology of Freshwater Fish* 25:664–673. https://doi.org/10.1111/eff.12244

Foley, K., Rosenberger, A., and Mueter, F. 2015. Effectiveness of single-pass backpack electrofishing to estimate juvenile coho salmon abundance in Alaskan headwater streams. *Fisheries Science* 81(4):601–610. https://doi.org/10.1007/s12562-015-0888-1

Gortázar, J., Alonso, C., and García de Jalón, D. 2012. Brown trout redd superimposition in relation to spawning habitat availability. *Ecology of Freshwater Fish* 21:283–292. https://doi.org/10.1111/j.1600-0633.2011.00546.x

Gortázar, J., García de Jalón, D., Alonso-González, C., Vizcaíno, P., Baeza, D., and Marchamalo, M. 2007. Spawning period of a southern brown trout population in a highly unpredictable stream. *Ecology of Freshwater Fish* 16:515–527. https://doi.org/10.1111/j.1600-0633.2007.00246.x

Harding, J. S., Clapcott, J. E., Quinn, J. M., Hayes, J. W., Joy, M. K., Storey, R. G., Greig, H. S., Hay, J., James, T., Beech, M. A., Ozane, R., Meredith, A. S., and Boothroyd, I. K. D. 2009. Stream habitat assessment protocols for wadeable rivers and streams of New Zealand. University of Canterbury Press, Christchurch, New Zealand.

Hayes, J. W. 1988. Comparative stream residence of juvenile brown and rainbow trout in a small lake inlet tributary, Scotts Creek, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 222:181–188. https://doi.org/10.1080/00288330.1988.9516290

Hayes, J. W. 1995. Spatial and temporal variation in the relative density and size of juvenile brown trout in the Kakanui River, North Otago, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 29(3):393–407. https://doi.org/10.1080/00288330.1995.9516674

Hayes, J. W., Olsen, D. A., and Hay, J. 2010. The influence of natural variation in discharge on juvenile brown trout population dynamics in a nursery tributary of the Motueka River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 44(4):247–269. https://doi.org/10.1080/00288330.2010.509905

Heggenes, J., Baglinière, J. L., and Cunjak, R. A. 1999. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. *Ecology of Freshwater Fish* 8:1–2. https://doi.org/10.1111/j.1600-0633.1999.tb00048.x

Hobbs, D. F. 1940. Natural reproduction of trout in New Zealand and its relation to density of populations. New Zealand Marine Department, Fisheries Bulletin 8, 93 pp.

Hobbs, D. F. 1948. Trout fisheries in New Zealand. Their development and management. New Zealand Marine Department, Fisheries Bulletin 9, 175 pp.

Holmes, R., Hayes, J. W., Jiang, W., Quarterman, A., and Davey, L. N. 2014. Emigration and mortality of juvenile brown trout in a New Zealand headwater tributary. *Ecology of Freshwater Fish* 23:631–643. https://doi.org/10.1111/eff.12118

Holmes, R., Matthaei, C., Gabrielsson, R., Closs, G., and Hayes, J. 2018. A decision support system to diagnose factors limiting stream trout fisheries. *River Research and Applications* 34:816–823. https://doi.org/10.1002/rra.3292

Hubert, W. A., Harris, D. D., and Wesche, T. A. 1994. Diurnal shifts in use of summer habitat by age-0 brown trout in a regulated mountain stream. *Hydrobiologia* 284:147–156. https://doi.org/10.1007/BF00006886

Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. *Limnology and Oceanography* 41:243–252. https://doi.org/10.4319/lo.1996.41.2.0243

Huntsman, B. M. and Petty, J. T. 2014. Density-dependent regulation of brook trout population dynamics along a core-periphery distribution gradient in a central appalachian watershed. *PLoS ONE* 9(3):e91673. https://doi.org/10.1371/journal.pone.0091673

Jenkins, T. M. Jr, Diehl, S., Kratz, K. W., and Cooper, S. D. 1999. Effects of population density on individual growth of brown trout in streams. *Ecology* 80:941–956. https://doi.org/10.2307/177029

Jones, D. A., Akbaripasand, A., Nakagawa, S., and Closs, G. 2019. Landscape features determine brown trout population structure and recruitment dynamics. *Ecology of Freshwater Fish* 28:554–562. https://doi.org/10.1111/eff.12474

Jonsson, N. and Jonsson, B. 1999. Trade-off between egg mass and egg number in brown trout. *Journal of Fish Biology* 55:767–783. https://doi.org/10.1111/j.1095-8649.1999.tb00716.x

Jonsson, B. and Jonsson, N. 2011. Ecology of Atlantic salmon and brown trout: habitat as a template for life histories. Springer, Dordrecht, Heidelberg, London, New York. https://doi.org/10.1007/978-94-007-1189-1

Jowett, I. G. 1990. Factors related to the distribution and abundance of brown and rainbow trout in New Zealand clear-water rivers. *New Zealand Journal of Marine and Freshwater Research* 24(3):429–440. https://doi.org/10.1080/00288330.1990.9516434

Jowett, I. G. 1993. A method for objectively identifying pool, run, and riffle habitats from physical measurements. *New Zealand Journal of Marine and Freshwater Research* 272:241–248. https://doi.org/10.1080/00288330.1993.9516563

Jowett, I. G. 1995. Spatial and temporal variability in brown trout abundance: A test of regression models. *Rivers* 5:1–12. https://doi.org/10.1080/00288330.1995.9516674

Jowett, I. G., Hayes, J. W., and Duncan, M. J. 2008. A guide to instream habitat survey methods and analysis. NIWA Science and Technology Series, 54, Wellington.

Jowett, I. G. and Richardson, J. 1989. Effects of severe flood on instream habitat and trout populations in seven New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 23:11–17. https://doi.org/10.1080/00288330.1989.9516335

Jowett, I. G. and Richardson, J. 2008. Habitat use by New Zealand fish and habitat suitability models. NIWA Science and Technology Series, 55, Wellington.

Keeley, E. R. 2003. An experimental analysis of self-thinning in juvenile steelhead trout. *Oikos* 102:543–550. https://doi.org/10.1034/j.1600-0706.2003.12035.x

Kondolf, G. M. and Wolman, M. G. 1993. The sizes of salmonid spawning gravels. *Water Resources Research* 29(7):2275–2285. https://doi.org/10.1029/93WR00402

Kristensen, E. A. and Closs, G. P. 2008a. Environmental variability and population dynamics of juvenile brown trout (*Salmo trutta*) in an upstream and downstream reach of a small New Zealand river. *New Zealand Journal of Marine and Freshwater Research* 42(1):57–71. https://doi.org/10.1080/00288330809509936

Kristensen, E. A. and Closs, G. P. 2008b. Variation in growth and aggression of juvenile brown trout (*Salmo trutta*) from upstream and downstream reaches of the same river. *Ecology of Freshwater Fish* 17:130–135. https://doi.org/10.1111/j.1600-0633.2007.00266.x

Kristensen, E. A., Closs, G. P., Olley, R., Kim, J., Reid, M., and Stirling, C. 2011. Determining the spatial distribution of spawning by anadromous and resident brown trout *Salmo trutta* L using strontium content of eggs collected from redds. *Ecology of Freshwater Fish* 20(3):377–383. https://doi.org/10.1111/j.1600-0633.2010.00451.x

Kruse, C. G., Hubert, W. A., and Rahel, F. J. 1998. Single-pass electrofishing predicts trout abundance in mountain streams with sparse habitat. *North American Journal of Fisheries Management* 18(4):940–946. https://doi.org/10.1577/1548-8675(1998)018<0940:SPEPTA>2.0.CO;2

Landergren, P. 2004. Factors affecting early migration of sea trout *Salmo trutta* parr to brackish water. *Fisheries Research* 67(3):283–294. https://doi.org/10.1016/j.fishres.2003.10.005

Lobón-Cerviá, J. 2008. Habitat quality enhances spatial variation in the self-thinning patterns of stream-resident brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 65(9):2006–2015. https://doi.org/10.1139/F08-105

Lobón-Cerviá, J. and Sanz, N. 2017. Brown trout: biology, ecology and management. John Wiley and Sons, Hoboken, NJ. https://doi.org/10.1002/9781119268352

Lobón-Cerviá, J., Rasmussen, G. H., and Mortensen, E. 2017. Discharge-dependent recruitment in stream spawning brown trout; pp. 297–318 in Brown Trout: Biology, Ecology and Management, Eds J. Lobón-Cerviá and N. Sanz. John Wiley and Sons, Hoboken, NJ. https://doi.org/10.1002/9781119268352.ch13

Louhi, P., Mäki-Petäys, A., and Erkinaro, J. 2008. Spawning habitat of Atlantic salmon and brown trout: general criteria and intragravel factors. *River Research and Applications* 24(3):330–339. https://doi.org/0.1002/rra.1072

Lund, E., Olsen, E. M., and Vøllestad, L. A. 2003. First-year survival of brown trout in three Norwegian streams. *Journal of Fish Biology* 62:323–340. https://doi.org/10.1046/j.1095-8649.2003.00025.x

Mikheev, P., Jarvis, M. G., Matthaei, C. D., Ingram, T., Nikiforov, A. I., and Closs, G. P. 2020. Geomorphological features drive spatiotemporal dynamics of young-of-the-year brown trout populations in a large New Zealand river catchment. *Freshwater Biology* 65:1392–1400. https://doi.org/10.1111/fwb.13507

Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271–287. https://doi.org/10.2307/1939533

Mutshinda, C. M., O'Hara, R. B., and Woiwod, I. P. 2009. What drives community dynamics? *Proceedings of the Royal Society B: Biological Sciences* 276(1669):2923–2929. https://doi.org/0.1098/rspb.2009.0523

Nicola, G. G. and Almòdovar, A. 2002. Reproductive traits of stream-dwelling brown trout *Salmo trutta* in contrasting neighbouring rivers of central Spain. *Freshwater Biology* 47:1353–1365. https://doi.org/10.1046/j.1365-2427.2002.00866.x

O'Briain, R., Coghlan, B., Shephard, S., and Kelly, F. L. 2019. River modification reduces climate resilience of brown trout (*Salmo trutta)* populations in Ireland. *Fisheries Management and Ecology* 26:512–526. https://doi.org/10.1111/fme.12326

Ottaway, E. M., Carling, P. A., Clarke, A., and Reader, N. A. 1981. Observations on the structure of brown trout, *Salmo trutta* Linnaeus, redds. *Journal of Fish Biology* 19:593–607. https://doi.org/10.1111/j.1095-8649.1981.tb03825.x

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.r-project.org

Richard, A., Cattaneo, F., and Rubin, J. F. 2015. Biotic and abiotic regulation of a low-density stream-dwelling brown trout (*Salmo trutta* L.) population: effects on juvenile survival and growth. *Ecology of Freshwater Fish* 24(1):1–14. https://doi.org/10.1111/eff.12116

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* 119:1–382.

Rubin, J., Glimsäter, C., and Jarvi, T. 2005. Spawning characteristics of the anadromous brown trout in a small Swedish stream. *Journal of Fish Biology* 66:107–121. https://doi.org/10.1111/j.0022-1112.2005.00586.x

Sánchez-Hernández, J., Shaw, S. L., Cobo, F., and Allen, M. S. 2016. Influence of a minimum-length limit regulation on wild brown trout: an example of recruitment and growth overfishing. *North American Journal of Fisheries Management* 36(5):1024–1035. https://doi.org/10.1080/02755947.2016.1184204

Santiago, J. M., García de Jalón, D., Alonso, C., Solana, J., Ribalaygua, J., Pórtoles, J., and Monjo, R. 2015. Brown trout thermal niche and climate change: expected changes in the distribution of cold-water fish in central Spain. *Ecohydrology* 9:514–528. https://doi.org/10.1002/eco.1653

Slavík, O., Horký, P., Randák, T., Balvín, P., and Bílý, M. 2012. Brown trout spawning migration in fragmented central European headwaters: Effect of isolation by artificial obstacles and the moon phase. *Transactions of the American Fisheries Society* 141:673–680. https://doi.org/10.1080/00028487.2012.675897

Syrjänen, J. T., Ruokonen, T. J., Ketola, T., and Valkeajärvi, P. 2015. The relationship between stocking eggs in boreal spawning rivers and the abundance of brown trout parr. *ICES Journal of Marine Sciences* 72(5):1389–1398. https://doi.org/10.1093/icesjms/fsv017

Velez-Espino, L. A., McLaughlin, R. L., and Robillard, M. 2013. Ecological advantages of partial migration as a conditional strategy. *Theoretical Population Biology* 85:1–11. https://doi.org/10.1016/j.tpb.2013.01.004

Vøllestad, L. A. and Olsen, E. M. 2008. Non-additive effects of density dependent and density-independent factors on brown trout vital rates. *Oikos* 117:1752–1760. https://doi.org/10.1111/j.1600-0706.2008.16872.x

Wolf, P. 1951. A trap for the capture of fish and other organisms moving downstream. *Transactions of the American Fisheries Society* 80:41–45. https://doi.org/10.1577/1548-8659(1950)80[41:ATFTCO]2.0.CO;2

Ye, Y. and Carocci, F. 2019. Control mechanisms and ecosystem-based management of fishery production. *Fish and Fisheries* 20:15–24. https://doi.org/10.1111/faf.12321

Zimmer, M. P. and Power, M. 2006. Brown trout spawning habitat selection preferences and red characteristics in the Credit River, Ontario. *Journal of Fish Biology* 68:1333–1346. https://doi.org/10.1111/j.0022-1112.2006.00995.x

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics* 12:163–169. https://doi.org/10.2307/3001759