

Hydrological drought and the role of refugia in an endangered riffle-dwelling fish, Nooksack dace (*Rhinichthys cataractae* ssp.)

Stephanie Avery-Gomm, Jordan S. Rosenfeld, John S. Richardson, and Michael Pearson

Abstract: Understanding the impacts of hydrological drought, and the role that refugia play in mitigating these impacts, is crucial to the conservation of freshwater fishes. This is especially true for species adapted to riffles, which are typically the first habitats to dewater at low discharge. We examined the relationship among decreasing stream discharge, abundance, and habitat use for Nooksack dace (*Rhinichthys cataractae* ssp.), an endangered riffle-dwelling species. A complementary experimental manipulation examined the effects of flow on growth rate across a discharge gradient in riffle and pool habitats. We found that low-velocity habitats and decreased discharge in experimental channels result in reduced dace growth and that decreasing stream flow was coincident with declines in Nooksack dace abundance. This study demonstrates the sensitivity of Nooksack dace to hydrological drought, and insofar as Nooksack dace are ecologically typical of small riffle-dwelling invertivore fishes, our results suggest that use of pools does not mitigate sublethal effects of declining flows on growth, although pools may provide refuge from the most negative effects of drought (i.e., stranding of fish).

Résumé : La compréhension des impacts de la sécheresse hydrologique et du rôle des refuges dans l'atténuation de ces impacts est un aspect clé de la conservation des poissons d'eau douce, en ce qui concerne tout particulièrement les espèces adaptées aux radiers, normalement les premiers habitats à s'assécher en situation de faible débit. Nous avons examiné la relation entre la diminution du débit d'un cours d'eau et l'abondance et l'utilisation de l'habitat par le naseux de la Nooksack (*Rhinichthys cataractae* ssp.), une espèce en voie de disparition qui fréquente les radiers. Une manipulation expérimentale complémentaire a permis d'examiner les effets de l'écoulement sur le taux de croissance le long d'un gradient de débit dans des habitats de radiers et fosses. Nous avons constaté que les habitats de faible vitesse d'écoulement et un débit réduit dans les lits expérimentaux se traduisaient par une croissance plus faible des naseux, et qu'un débit réduit coïncidait avec des baisses de l'abondance des naseux de la Nooksack. L'étude démontre la sensibilité des naseux de la Nooksack à la sécheresse hydrologique et, dans la mesure où ces poissons sont typiques, sur le plan écologique, des poissons invertivores qui fréquentent les radiers, nos résultats donnent à penser que l'utilisation de fosses n'atténue pas les effets sublétaux de la réduction des débits sur la croissance, bien que les fosses puissent servir de refuge contre les effets les plus néfastes de la sécheresse (c.-à-d. l'échouage de poissons). [Traduit par la Rédaction]

Introduction

Extinction rates for species in fresh water are exceedingly high (Ricciardi and Rasmussen 1999), and in North America alone the number of imperiled freshwater fishes increased by 92% between 1989 (364 species; Williams et al. 1989) and 2008 (700 species; Jelks et al. 2008). A variety of stressors are responsible for this trend, but arguably the most important is flow modification (Poff et al. 1997; Dudgeon et al. 2006), which includes a global trend of decreasing stream flow driven by climate-induced changes in precipitation patterns, increased evapotranspiration, and a rapidly growing human population that is impacting water availability through dams, diversions, and water withdrawals (Dai et al. 2009; Vörösmarty et al. 2000, 2010; Dai 2012). In many areas, the result has been an increase in the frequency and intensity of hydrological droughts (Postel and Richter 2003; IPCC 2007; Kundzewicz et al. 2008), which may be defined as deficiencies in water supplies as measured by declines in stream discharges, lake, reservoir, or ground-water levels (Smakhtin 2001). Hydrological drought is a disturbance that reduces habitat area, lateral connectivity between mainstem

and floodplain habitats, and water quality (Magoulick and Kobza 2003), which in turn affects ecosystem function, community structure, population dynamics, and in extreme cases may cause local or global extinction (Kushlan 1976; Xenopoulos et al. 2005). Understanding the impacts of hydrological drought is essential to the conservation of freshwater fish, particularly in areas where demand for consumptive water use is high and likely to rise.

Drought affects habitat types differently and may severely alter relative habitat availability (e.g., ratio of pools to riffles). In shallow, fast-flowing riffle habitats, velocity, depth, and habitat area decrease, and in extreme cases riffle habitats may dry completely. Pools also shrink in size, but retain water for longer after cessation of surface flow (Hakala and Hartman 2004). During drought, environmental conditions in both habitats may be characterized by increases in physicochemical extremes of temperature, dissolved oxygen, pH, and nutrient loading (reviewed in Lake 2003). Drought also increases density-dependent biotic interactions such as predation and competition (Power 1984, 1987; Harvey and

Received 8 November 2013. Accepted 23 June 2014.

Paper handled by Associate Editor Michael Bradford.

S. Avery-Gomm. Department of Zoology, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

J.S. Rosenfeld. Ministry of Environment, Province of British Columbia, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada.

J.S. Richardson. Department of Forest and Conservation Sciences, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

M. Pearson. Pearson Ecological, 2840 Lougheed Highway, Agassiz, BC V0M 1A1, Canada.

Corresponding author: Stephanie Avery-Gomm (e-mail: Stephanie.AveryGomm@gmail.com).

Authors listed in order of contribution.

Stewart 1991), as fish are crowded into a reduced habitat volume (Matthews and Marsh-Matthews 2003).

Most stream fishes have a discrete range of habitat preferences defined by abiotic characteristics such as depth, velocity, temperature, and dissolved oxygen (i.e., the ecological niche; Hutchinson 1957). As stream discharge decreases, deteriorating water quality conditions may exceed tolerance thresholds, forcing fish to seek refugia (Grossman and Ratajczak 1998; Hodges and Magoulick 2011). These can be defined spatially as locations where the negative effects of disturbance are lower than in the surrounding environment (Lancaster and Belyea 1997). For example, as discharge decreases, riffle specialists may abandon riffles and seek refuge in pools (Gelwick 1990), though the relative value of pools will likely depend on factors such as abiotic suitability, prey availability, and predation risk (Power 1987; Schaefer 2001). The role that low-flow refugia play in mitigating the negative effects of drought in terms of population persistence and individual performance is not well understood, particularly for riffle-dwelling species (Magoulick and Kobza 2003).

In this study we used a combination of field observations and experimental manipulations to quantify the impacts of drought and explore the role that refugia play in mitigating these impacts for Nooksack dace (Cyprinidae: *Rhinichthys cataractae* ssp.), a riffle-specialist endemic to northwestern Washington and southwestern British Columbia. In Canada, Nooksack dace are federally listed as endangered (COSEWIC 2007; Pearson et al. 2008), and populations are threatened by hydrological drought, due in part to surface and groundwater withdrawals (Pearson 2004; Golder Associates Ltd. 2005). Low-flow effects on dace were assessed by first quantifying seasonal changes in Nooksack dace abundance and habitat use in a temperate coastal stream as a function of decreasing stream discharge. We hypothesized that if Nooksack dace use pool habitats as refugia during hydrological drought, then dace would emigrate out of riffles and into pools, which would manifest as a seasonal decrease in Nooksack dace abundance in riffles and a corresponding increase in both the abundance and density of Nooksack dace in pools. Second, to assess the direct effects of hydrological drought on Nooksack dace performance and the relative value of pools as refugia, we measured dace growth in experimental riffles and pools across a range of discharges. Benthic prey are a key resource for riffle-dwelling invertivores, and studies have demonstrated that benthic invertebrate abundance is flow-sensitive (e.g., Minshall and Winger 1968; Cowx et al. 1984). Consequently, benthic invertebrate biomass was quantified in experimental habitats so that the relationship between prey availability and growth rate could be examined.

Methods

Study site

Research took place in the Canadian portions of Bertrand Creek and Pepin Creek, two regulated transboundary lowland watercourses in southwestern British Columbia that flow south into Washington State, USA. Stream gradients average 1%–2% and bankfull widths for these watercourses are 6.6 ± 0.4 and 15.4 ± 4.4 m, respectively (Pearson 1998). Mean annual discharge (MAD) is $1.15 \text{ m}^3 \cdot \text{s}^{-1}$ for Bertrand Creek and $0.42 \text{ m}^3 \cdot \text{s}^{-1}$ for Pepin Creek. The coastal climate in this temperate region is characterized by warm, dry summers and mild, wet winters with high annual precipitation ($1573 \text{ mm} \cdot \text{year}^{-1}$; Environment Canada 2002). The majority of precipitation falls from October to May, and from June to September baseflow is largely maintained by groundwater contributions from the Abbotsford–Sumas Aquifer (Berg and Allen 2007). Minimum monthly flows for the July to October period of

these two streams (i.e., critical period stream flow; Binns 1982) is $0.046 \text{ m}^3 \cdot \text{s}^{-1}$ (4% MAD) in Bertrand Creek and $0.145 \text{ m}^3 \cdot \text{s}^{-1}$ in Pepin Creek (35% MAD; Environment Canada 2012; USGS 2012; R.A. Ptolemy, personal communication, 2013). Both streams are increasingly susceptible to hydrological drought (Pearson 2004). Particularly in Bertrand Creek, increases in surface and groundwater withdrawals have reduced present-day baseflows by 20% below historical values (Golder Associates Ltd. 2005). There are a number of co-occurring species in these streams, including coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), rainbow and steelhead trout (*Oncorhynchus mykiss*), coho salmon (*Oncorhynchus kisutch*), western brook lamprey (*Lampetra richardsoni*), threespine stickleback (*Gasterosteus aculeatus*), largescale sucker (*Catostomus macrocheilus*), longnose sucker (*Catostomus catostomus*), prickly sculpin (*Cottus asper*), and American signal crayfish (*Pacifastacus leniusculus*). Introduced species include largemouth bass (*Micropterus salmoides*), pumpkinseed (*Lepomis gibbosus*), and brown bullhead (*Ameiurus nebulosus*).

Flow effects on Nooksack dace habitat use and abundance

Site selection

To determine the effects of hydrological drought on Nooksack dace abundance and habitat use, a field study was conducted in Bertrand Creek from May to August 2010. Bertrand Creek drains a 46.6 km^2 low-elevation watershed dominated by agriculture, before flowing south into the United States where it enters the Nooksack River (Pearson 2004; Environment Canada 2012). Four reaches of Bertrand Creek, previously identified as having high-quality Nooksack dace habitat and federally designated as Critical Habitat under the Species At Risk Act (i.e., >10% riffle habitat by length; Pearson et al. 2008), were selected as focal reaches for this study (see online Supplementary Material, Fig. S1¹). These were of similar length (mean \pm SD, 137.5 ± 48.6 m), bankfull width (7.5 ± 1.8 m) and gradient (1%–2%) (see online Supplementary Material, Table S1¹). Within each focal reach, pool and riffle habitat units were identified and a minimum of three riffles and three pools was randomly selected (Johnston and Slaney 1996). During the 2010 sampling period, flows in Bertrand Creek were exceptionally low, with cessation of surface flow in one reach. Minimum monthly summer flows were $0.014 \text{ m}^3 \cdot \text{s}^{-1}$ or 1.2% of MAD, compared with a 23-year mean minimum monthly summer flow of $0.046 \text{ m}^3 \cdot \text{s}^{-1}$ (Environment Canada 2012).

Sampling methods

Each habitat unit was stop-netted and serially sampled over a range of declining discharges (i.e., three times, between 0.113 and $0.007 \text{ m}^3 \cdot \text{s}^{-1}$) from May to August 2010. Stream discharge was estimated in each habitat using the Riverine Habitat Simulation Model software (RHABSIM; Payne 1994; Scruton et al. 1998) using depth and velocity data collected along transects with a Marsh-McBirney Flo-Mate 2000 velocity meter (Hach Company, Loveland, California). Pool habitats were seined (triple-pass) and riffle habitats were sampled using single-pass electrofishing upstream of a modified Fyke stop-net (see online Supplementary Material, Fig. S2¹), which was effective for catching benthic riffle-dwelling fish that were swept downstream into the bucket of the net. Multiple-pass electrofishing was avoided to minimize harm to this endangered species (Pearson 2009). Different gear were used in pools and riffles to maximize capture efficiency and confidence in population estimates; use of a single gear type in both habitats (e.g., electrofishing) would have introduced biases because of extremely low capture efficiency in deep pool habitat. Captured fish were identified and counted, and Nooksack dace greater than

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0585>.

40 mm fork length (± 1 and older age classes; Inglis et al. 1994) were measured to the nearest millimetre and weighed to the nearest 0.01 g.

Dace abundance in pools was estimated using the Schnute (1983) maximum likelihood procedure adapted to a three-pass depletion seining. Abundance of Nooksack dace in riffles was estimated by adjusting the number of dace captured by a capture efficiency factor that was calculated from seven two-stage mark-recapture experiments in representative riffles across a range of discharges (where capture efficiency is estimated as a function of mean water velocity; Appendix A). The abundance of Nooksack dace for each focal reach was calculated as the summed abundance of Nooksack dace within sampled pool and riffle habitat units within that reach, for each sampling event. Density in each sampled habitat unit was calculated as abundance divided by habitat area. Mean riffle and pool areas (\pm SD) were 38.4 ± 27.5 and 29.8 ± 17.5 m², respectively. Although the area of each sampled habitat unit declined with flow, the length of each habitat unit was constant across sampling periods. Effects of declining discharge on Nooksack dace at the habitat scale (i.e., riffle or pool) were therefore characterized both in terms of density (fish·m⁻²) and abundance (fish·habitat unit⁻¹), to control for flow-related changes in habitat area.

Data analysis

Within one of the four focal reaches, the number of Nooksack dace captured was very small (i.e., $N < 5$) despite high sampling effort and an abundance of riffle habitat with cobble and gravel substrate. Negligible abundance in this reach was likely a result of flow ceasing altogether at summer low flow, unlike the other study reaches where flowing water was always present. As the purpose of this study was to quantify how declining flow affects Nooksack dace density and abundance among habitats, this focal reach was deemed to have an insufficient population for meaningful statistics and so was excluded from further quantitative analysis. For the remaining focal reaches, repeated measures mixed effects analysis of covariance (ANCOVA) was used to evaluate the effects of focal reach, habitat type (riffle or pool; fixed) and discharge (m³·s⁻¹; covariate) on Nooksack dace abundance at the habitat scale (fish·habitat unit⁻¹) and density (fish·m⁻²), using the nlme package in R version 2.10.1 statistical software (R Development Core Team 2009; Pinheiro et al. 2009). Nooksack dace abundance was log₁₀-transformed to meet the assumption of homogeneity of variance, and covariance structure was modelled as Continuous AR(1) to account for autocorrelation of repeated samplings of the same habitat at different discharges.

Flow effects on Nooksack dace growth rate in experimental channels

Experimental design

Four parallel seminatural in-ground stream channels, each with two serial riffle-pool sequences (see online Supplementary Material, Fig. S3¹), were used to investigate the effects of low discharge on Nooksack dace growth in pools and riffles. These experimental channels were constructed as off-channel habitat in 2009 and received water diverted from the main stem of Pepin Creek. Channels were 20 m long and averaged 1.5 m wide. Discharge treatments of 3, 8, 15, and 27 L·s⁻¹ were chosen to represent a gradient from low- to high-quality dace habitat, based on published habitat suitability curves describing the relationship between depth and velocity and Nooksack dace abundance (Inglis et al. 1994). Each channel was randomly assigned a discharge treatment that was regulated using upstream weirs and monitored twice daily using discharge-calibrated staff gauges. Discharge was calculated by measuring depth and velocity along transects in each channel using a Marsh-McBirney Flo-Mate 2000 velocity meter (Hach Company, Loveland, California).

Prior to the start of the experiment, all fish (i.e., potential predators and competitors) were removed from the stream channels by electroshocking and seining, and 6 mm mesh galvanized steel fences were installed to ensure that Nooksack dace could not move between adjacent experimental riffle and pool habitat units. Channels were left fallow for 1 month to allow the natural substrate in the channels to be colonized by benthic invertebrates from Pepin Creek before the addition of Nooksack dace.

Sampling methods

The population of Nooksack dace in Pepin Creek is small, and conservation concerns precluded the collection of experimental fish from Pepin Creek. Instead, 109 Nooksack dace (mean (\pm SD) length: 72 ± 9 mm; mass: 4.39 ± 1.72 g) were captured in adjacent Bertrand Creek and transported to Pepin Creek where they were weighed, measured, and individually marked using ventral subcutaneous injections of visual implant elastomer (Northwest Marine Technologies, Inc.; Hill and Grossman 1987). Experimental fish were allowed to acclimate overnight before being stocked in experimental units at ambient densities of 0.75 fish·m⁻², which is well within the range of natural densities (Inglis et al. 1994; Pearson 2004; Avery-Gomm 2013). Higher densities were avoided to prevent density dependence from confounding habitat and flow effects on dace growth. Lightweight garden netting was stretched across riffles and staked into the ground to minimize vulnerability to terrestrial predators. After 33 days, Nooksack dace were recaptured and measured for length and mass.

To explore the relationship between flow and habitat effects on prey availability and Nooksack dace growth, three benthic invertebrate samples were collected in each experimental habitat immediately prior to collection of dace at the end of the experiment. A Hess sampler was used to collect benthic invertebrates in riffles. Because of the greater depth and negligible velocity in pools, benthic invertebrates in pools were sampled by carefully scooping surface sediment (i.e., to a depth no more than 3 cm) from a known area (0.0075 m²) into a 250 μ m mesh Surber sampler attached to the end of a pole. Invertebrates were preserved in 5% formalin and later identified to order (or family in the case of Hydropsychidae). Benthic invertebrate samples were dried at 60 °C for 24 h, weighed, and ash-free dry mass (g) was calculated after the dried sample was combusted in a muffle furnace at 500 °C for 1 h. Biomass (g) was standardized to an area of 1 m².

Invertebrate orders and families were classified as available prey if they had previously been recorded in the diet of Nooksack dace (McPhail 1997) or if they were observed in the stomachs of a subsample of 30 dace sampled using gastric lavage (see online Supplementary Material, Table S2¹) (Light et al. 1983). Available prey biomass per unit area (g·m⁻²) was calculated as the mean for the three benthic samples collected in each experimental unit.

HOBO temperature loggers (Onset Computer Corp., Bourne, Massachusetts) were used to record water temperature at 30 min intervals in the upstream riffle and downstream pool of each discharge treatment for the duration of the experiment. Dissolved oxygen was not measured during the experiment because a pilot study in 2010 showed that oxygen concentrations did not differ across discharge treatments and remained above 5 mg·L⁻¹, which is the federal guideline for the protection of aquatic life (CCREM 1987). Consequently, dissolved oxygen was not considered a factor limiting Nooksack dace growth in this experiment.

Data analysis

Individual fish growth rate (% body mass·day⁻¹) was calculated as

$$\text{Growth rate} = \left[\frac{\ln(\text{Mass}_{\text{after}}) - \ln(\text{Mass}_{\text{before}})}{\text{days}} \right] \times 100$$

and mean growth rate was calculated for each experimental unit. To test the hypotheses that growth rates would be higher in riffles than in pools and that growth would be negatively impacted by low flow, we modelled mean growth rate (\log_{10} -transformed) as a function of discharge, habitat type (two levels: riffle and pool), and a habitat \times discharge interaction using ANCOVA. ANCOVA was also used to evaluate whether prey availability (square-root-transformed) or mean water temperature were affected by discharge treatment or habitat type. Because the method used to sample benthic invertebrates in pool habitats may have included a large number of chironomids that were buried in sediment at depths inaccessible to foraging dace, we also analyzed discharge and habitat effects on chironomids separately, using ANCOVA to test for habitat-specific relationships between chironomid biomass ($\text{g}\cdot\text{m}^{-2}$) and discharge, and between dace growth rate and chironomid biomass.

To evaluate the factors that influenced Nooksack dace growth, stepwise model simplification was used with total prey biomass, mean temperature, depth, and velocity as independent predictor variables. At each step of analysis, variables were entered into the model if the significance level was less than 0.05 and removed if the significance level was greater than 0.10, terminating when no more variables were eligible for inclusion or removal (i.e., the minimal adequate model). For the purposes of comparison with the null hypothesis significance testing based on stepwise regression (Symonds and Moussalli 2011), and to identify uncertainty in the minimal adequate model, we also used model selection with the Akaike information criterion corrected for small sample sizes (AIC_c ; Akaike 1973). We considered candidate models as having good support when competing models were within $2 \Delta\text{AIC}_c$ of the best model (Burnham and Anderson 2002). Analyses were performed using R version 2.10.1 statistical software and the AICcmodavg package (R Development Core Team 2009; Mazerolle 2010).

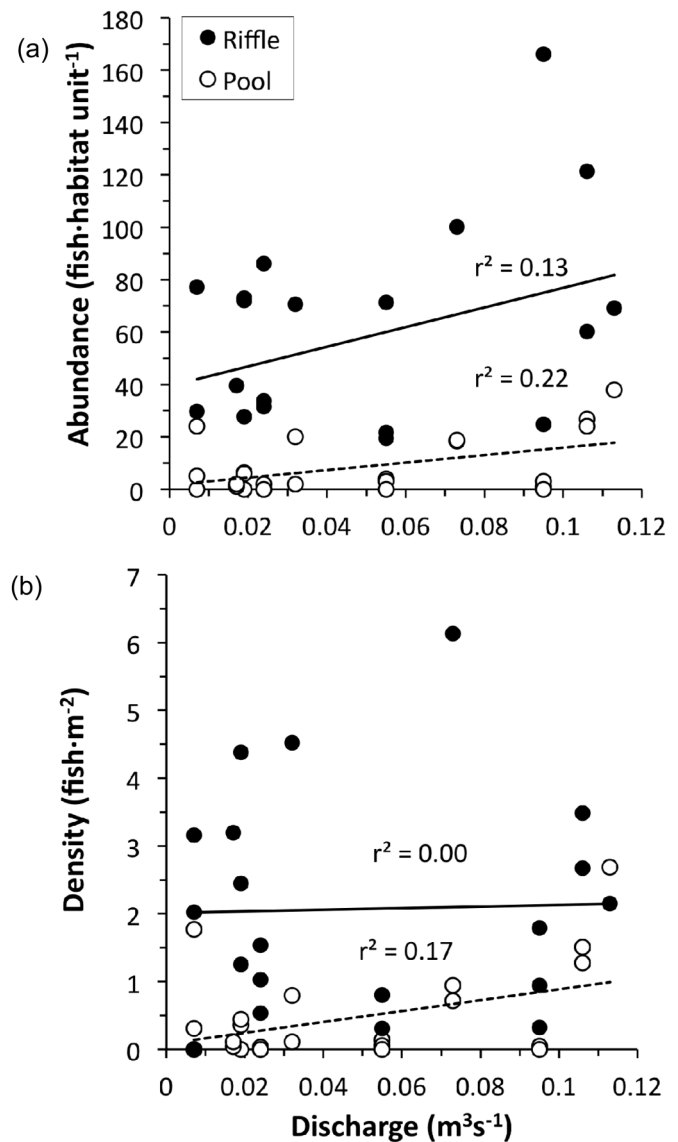
Results

Flow effects on Nooksack dace habitat use and abundance

Across all focal reaches and sampling dates, 458 Nooksack dace were captured by seining and electrofishing, representing an estimated total of 1470 fish throughout the study reaches (i.e., fish captures adjusted for capture efficiency; Appendix A). Captured fish had a mean ($\pm\text{SD}$) length of 61.6 ± 12.0 mm and a mass of 2.82 ± 1.76 g (length-mass regression: $\text{mass (g)} = 2 \times 10^{-5} \times \text{length (mm)}^{2.81}$; $r^2 = 0.91$). Across all sampling events, Nooksack dace densities averaged three times higher in riffles than in pools (2.04 and 0.68 fish $\cdot\text{m}^{-2}$, respectively; $F_{[1,11]} = 7.84$, $P = 0.02$), and densities were significantly higher in the 248th and Farm focal reaches than in the 0 Avenue reach ($F_{[1,11]} = 4.30$, $P = 0.04$; see online Supplementary Material, Table S3). There was one notable outlier, a single pool habitat in the 248th focal reach. Within this pool, Nooksack dace densities ranged from 10.0 to 6.2 to 3.2 fish $\cdot\text{m}^{-2}$ over the three sampling periods, which is considerably higher than the range of mean densities reported in previous studies (0.65 – 1.9 fish $\cdot\text{m}^{-2}$; Inglis et al. 1994; Pearson 1999; Bonamis 2011), where dace were found to be consistently less abundant in pools than in riffles. This pool also had the highest recorded density of dace in any sampled habitat in this study and was 5.0 standard deviations greater than mean densities in pool habitat in the sampled reach and 5.3 standard deviations higher than the reach mean. This anomalous habitat unit was therefore excluded from the analysis because it was a strong statistical and ecological outlier. Ecological reasons underlying this anomalous pool density are considered in the Discussion.

As summer flows declined from 0.113 to 0.007 $\text{m}^3\cdot\text{s}^{-1}$ across the three sampling dates, total habitat area decreased by 12.5% . Water depth and velocity decreased considerably over the summer low-flow period in both pools and riffles. Decline in mean ($\pm\text{SD}$) riffle velocity was more pronounced, decreasing from the first and last

Fig. 1. Observed changes in (a) Nooksack dace abundance and (b) Nooksack dace density (fish $\cdot\text{m}^{-2}$) in riffle (solid circles) and pool (open circles) habitats units in Bertrand Creek, sampled over a range of discharges (0.113 to 0.007 $\text{m}^3\cdot\text{s}^{-1}$).



sampling periods from 0.26 ± 0.06 to 0.09 ± 0.03 $\text{m}\cdot\text{s}^{-1}$. Nooksack dace abundance within the repeatedly sampled riffle and pool habitats decreased significantly (Fig. 1a; $F_{[1,14]} = 11.05$, $P < 0.01$). Contrary to expectations regarding use of pools as a low-flow refugia, the decrease in Nooksack dace abundance in riffles with declining stream discharge was not matched by a concomitant widespread increase in Nooksack dace abundance ($F_{[1,14]} = 1.46$, $P = 0.24$) or density in pools ($F_{[1,14]} = 0.04$, $P = 0.85$). Rather, there was a nonsignificant decrease in Nooksack dace density in both riffles and pools (Fig. 1b; $F_{[1,4]} = 0.99$, $P = 0.33$) associated with declining discharge. This apparent paradox of a significant decline in fish abundance but not density is partly due to the fact that both fish abundance and surface area of habitat declined with flows, thereby tending to maintain densities.

Flow effects on Nooksack dace growth rate in experimental channels

Ninety-eight of the experimental Nooksack dace (90% of stocked fish) were recovered alive at the end of the experiment and re-

turned to their place of origin, three dace were found dead showing signs of predation, and eight fish were not recovered. Mean growth rates for Nooksack dace in experimental habitats ranged from -0.02 to $0.99\% \cdot \text{day}^{-1}$. There was no significant main effect of discharge ($F_{[1,12]} = 0.73$, $P = 0.41$) or habitat type ($F_{[1,12]} = 4.53$, $P = 0.055$) on Nooksack dace growth rate; however, there was a significant habitat \times discharge interaction (Fig. 2; $F_{[1,12]} = 5.99$, $P = 0.03$). Nooksack dace growth rates were highest in high-flow riffle habitats ($0.84 \pm 0.16\% \cdot \text{day}^{-1}$) and were negatively influenced by low flow ($0.39 \pm 0.07\% \cdot \text{day}^{-1}$). In contrast, mean (\pm SD) growth rates in pools were about half of the maximum in riffles ($0.36 \pm 0.18\% \cdot \text{day}^{-1}$) and did not vary significantly with discharge ($0.25 \pm 0.38\% \cdot \text{day}^{-1}$ at high flow versus $0.40 \pm 0.23\% \cdot \text{day}^{-1}$ at low flow).

Mean water temperatures in the experimental habitats ranged from 12.8 to 15.4 °C and tended to be higher in the lowest discharge treatment, although there was no significant discharge effect ($F_{[1,4]} = 1.94$, $P = 0.24$) or habitat effect ($F_{[1,4]} = 0.03$, $P = 0.87$) on temperature and no significant habitat \times discharge interaction ($F_{[1,4]} = 0.01$, $P = 0.93$). Taxa included in available prey biomass ($\text{g} \cdot \text{m}^{-2}$) included Amphipoda, Chironomidae, Ephemeroptera, Elmidae, Hydropsychidae, Ostracoda, Plecoptera, Simuliidae, and Tipulidae. Available prey biomass was significantly higher in pools than in riffles (Fig. 3; $F_{[1,12]} = 99.97$, $P < 0.01$), but did not vary significantly with discharge ($F_{[1,12]} = 3.98$, $P = 0.07$), and there was no significant interaction between habitat and discharge ($F_{[1,12]} < 0.01$, $P = 0.96$). Prey biomass was dominated by chironomids (38%–57% of prey biomass in riffles and 52%–90% of prey biomass in pools).

Multiple regression with stepwise selection indicated that neither prey biomass nor mean water temperature were significant predictors of Nooksack dace growth rate (growth rate = velocity; $r^2 = 0.25$, $P = 0.03$, $n = 16$). This was supported by AIC_c model selection, which identified velocity effects on growth as the best model (i.e., no other models were within $2 \Delta\text{AIC}_c$; see online Supplementary Material, Table S4¹). When analyzed separately, chironomid biomass ($\text{g} \cdot \text{m}^{-2}$) was significantly higher in pools than in riffles (Fig. 4a; $F_{[1,12]} = 28.82$, $P < 0.01$). Despite being a primary prey item for Nooksack dace, there was no significant overall relationship between Nooksack dace growth rate and chironomid biomass ($F_{[1,12]} = 1.88$, $P = 0.20$), although a significant habitat \times discharge interaction indicated that chironomid biomass was correlated with growth rate in riffles, but not in pools (Fig. 4b; $F_{[1,12]} = 1.88$, $P < 0.05$).

Discussion

In this study, we examined the effects of declining flows and hydrological drought on growth and abundance of Nooksack dace and the potential role of pools as low-flow refugia. A low growth rate among Nooksack dace in low discharge experimental riffles and a decline in dace abundance coincident with declining discharge in sampled reaches both indicate that hydrological drought has the potential for substantial negative impacts on Nooksack dace. We tested the hypothesis that Nooksack dace use pools as refugia by looking for evidence of increased use of pool habitats as flows declined, but a general elevation in dace abundance in pools was not supported across the observed range of flows. Additionally, growth rates were depressed in experimental pools at all flows, suggesting that pool habitats do not mitigate the sublethal effects of hydrological drought. Although pools may provide opportunities for increased survival when riffles dewater completely, collectively these two studies support the inference that pools provide poor quality refugia in terms of mitigating the negative effects of hydrological drought on individual performance.

Over the course of the summer low-flow period, abundance of fish in sampled habitats decreased by nearly half, suggesting a progressive degradation in abiotic or biotic conditions associated with drought (Lake 2003). Emigration of Nooksack dace out of the

Fig. 2. Effect of discharge ($\text{L} \cdot \text{s}^{-1}$) and habitat type (riffles: solid circles; pools: open circles) on Nooksack dace growth rate ($\% \cdot \text{day}^{-1}$). Logarithmic trend lines are consistent with the ANCOVA that was performed on \log_{10} -transformed growth data.

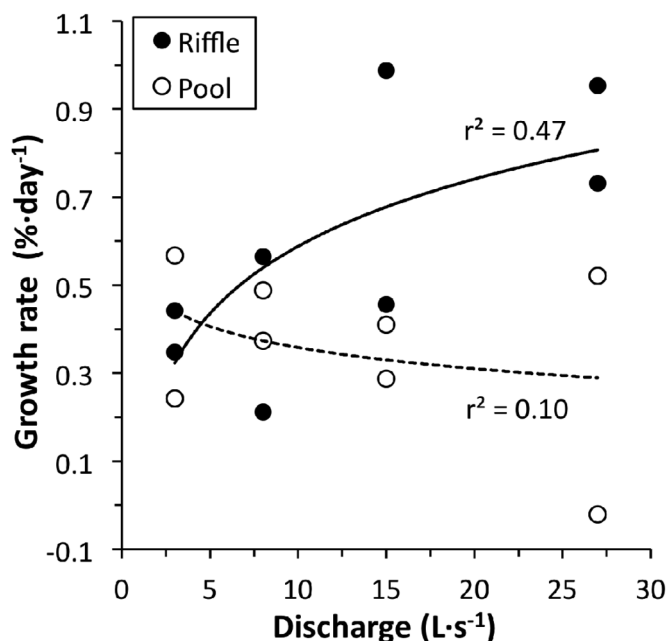
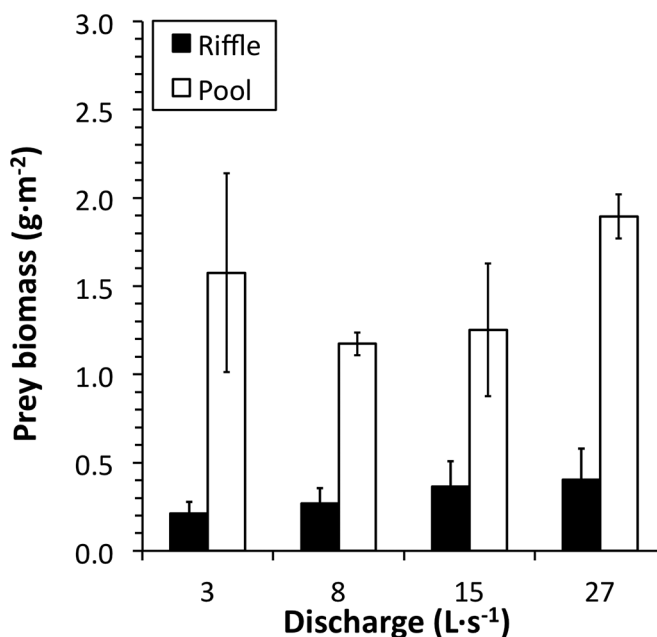
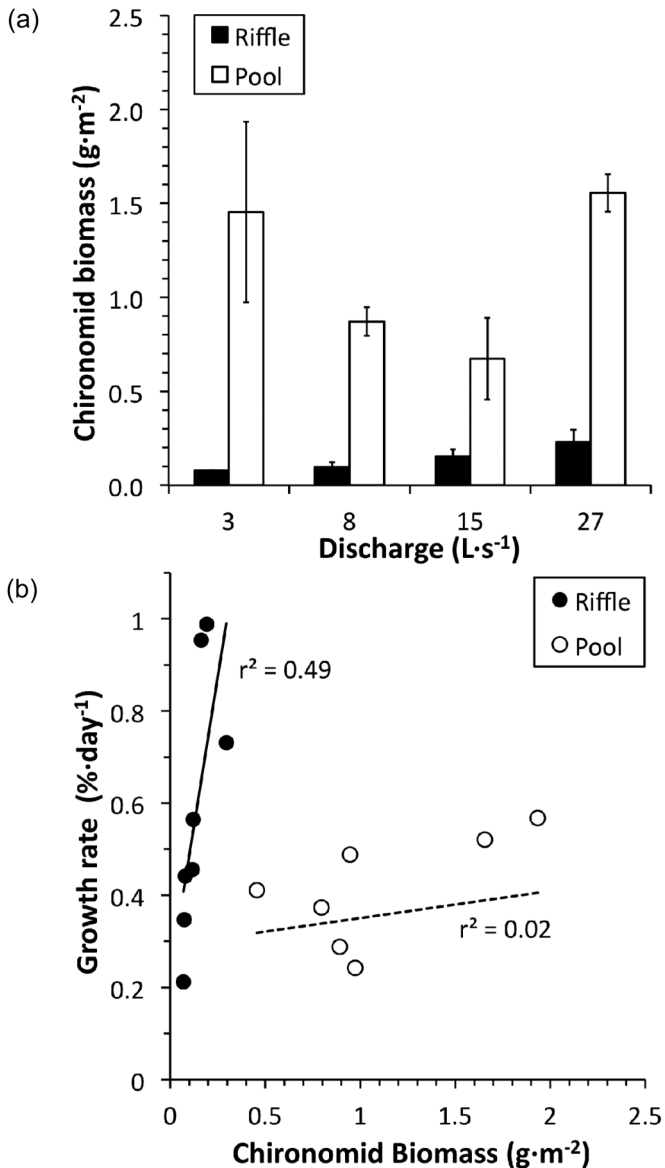


Fig. 3. Total biomass of benthic prey ($\text{g} \cdot \text{m}^{-2}$) in experimental riffle (solid bars) and pool (open bars) habitats across a gradient of discharges. Data are shown as means \pm SD.



focal reaches may have contributed to the observed temporal decline in measured abundance; however, the focal reaches included some of the highest quality dace habitat in Bertrand Creek and were separated by long reaches dominated by pool habitat. Schaefer (2001) and Lonzarich et al. (2000) found that long stretches of riffle deterred movements of pool-dwelling fish, and the opposite may be true for riffle-dwelling species. Additionally, Nooksack dace have been characterized as largely sedentary (i.e., having small home ranges of 50–100 m; Pearson 2004), consistent

Fig. 4. (a) Biomass of chironomids in experimental pool (open bars) and riffle habitats (solid bars) across a discharge gradient. (b) Growth rate of dace as a function of chironomid biomass in experimental pool (open circles) and riffle (solid circles) habitats.



with the documented home range sizes of the closely related longnose dace (Hill and Grossman 1987). Channel size and habitat quality downstream of the sampled reaches does not change appreciably until the confluence with the Nooksack River 10 km downstream; therefore, emigration alone seems unlikely to fully account for declines in dace abundance, though it is difficult to be certain without movement data.

An alternative driver of observed declines in Nooksack dace abundance is drought-related mortality. Reduced abundance due to mortality is a common effect of hydrological drought and is usually associated with adverse habitat conditions (Matthews and Marsh-Matthews 2003). These may include degradation of water quality (temperature, dissolved oxygen) or negative biotic interactions such as increased competition for food resources or vulnerability to predation in a reduced foraging arena (Matthews and Maness 1979; Power 1984; Power et al. 1985). Water temperatures in Bertrand Creek were well below the inferred thermal maximum of Nooksack dace (e.g., 31.4 °C as reported for the closely

related longnose dace; Brazo et al. 1978; Wismer and Christie 1987), and no obvious fish kills were observed, suggesting that degraded water quality did not cause direct mortality (e.g., Tramer 1977). However, other studies have shown that decreased water volumes can reduce the ability of fish to escape predation (Kushlan 1976; Power et al. 1985), and coastal cutthroat trout (known dace predators) are ubiquitous in pool habitat in Bertrand Creek and other coastal streams (e.g., Rosenfeld et al. 2000). In addition, herons and kingfishers were observed along the banks of Bertrand Creek, and evidence of predation on dace by terrestrial mammals (e.g., mink) was observed in experimental channels and confirmed by wildlife cameras in a subsequent study (M. Champion, personal communication, 2013). Although some Nooksack dace may have emigrated out of the focal reaches, increased vulnerability of Nooksack dace to aquatic and terrestrial predators seems an equally plausible mechanism for observed declines in abundance. However, without further study it cannot be definitively concluded that mortality-related declines in abundance were the result of drought-related decreases in habitat area (i.e., Kushlan 1976; Power et al. 1985). This highlights the challenges in interpreting the results of field studies where flow-related changes in fish abundance may be confounded by seasonal changes in movement or obscured by background mortality rates. Because mortality rates of small fish are relatively high (Lorenzen 1996), observed seasonal declines in dace abundance may conceivably be due to background mortality, independent of flow. Without a control stream that experiences no seasonal decline in discharge, it is difficult to distinguish between flow-independent mortality and apparent mortality associated with declining discharge. However, it is likely that decreased discharge is at least partly causative in elevating mortality rates, since drought-related reductions in wetted area and depth are commonly observed correlates of increased vulnerability to aquatic and terrestrial predators (Lonzarich and Quinn 1995; Power 1984; Power et al. 1985).

To better isolate the impacts of low flow on Nooksack dace while controlling for mortality related to predation risk, we quantified growth rates of Nooksack dace in experimental riffles and pools across a range of discharge treatments. Growth rates are a useful measure of individual performance and habitat quality, as larger size-at-age is associated with increased survivorship, maturation, and fecundity (Sogard 1997). Within experimental riffles, drought-like conditions had a negative effect on Nooksack dace growth rate, with fish in low discharge treatments growing at approximately half the rate of fish in high discharges treatments. In contrast, individual performance in pools was low irrespective of discharge. These results confirm that riffle habitats are intrinsically better for Nooksack dace than pools irrespective of predation risk, but highlight that habitat quality and individual performance in riffles is strongly flow-dependent. If refugia are defined as habitats where the negative effects of a disturbance are reduced relative to the surrounding habitat matrix (Lancaster and Belyea 1997), then pool habitats provide poor quality refugia in terms of mitigating the sublethal effects of hydrological drought on dace growth rate, until riffle habitat quality becomes severely degraded by low flows. Because predators like coastal cutthroat trout prefer pool habitat (Rosenfeld et al. 2000), elevated predation risk means that the realized growth potential of dace in Bertrand Creek pools is likely even lower than observed in our experimental channels where trout were absent. The limitations of pool habitat in mitigating the long-term effects of riffle loss are supported by the near absence of dace from the sample reach where discharge ceased altogether at low flow, despite abundant pool habitat at zero flow and abundant riffle at higher discharge.

Sublethal effects such as reduced growth can have a large impact on population dynamics (Rose 2000). One way to conceptualize the broader impacts of hydrological drought is to extrapolate annual growth of dace in high- and low-flow experimental riffles, based on the observed short-term growth rates. In low-flow riffles,

growth rates averaged $0.39\% \cdot \text{day}^{-1}$ compared with $0.84\% \cdot \text{day}^{-1}$ in high-flow riffles. Assuming that dace experience most of their growth in summer (mid-June to mid-September), when water temperatures are between 14.5 and 20.5 °C (McPhail 1997; USGS 2012), the cumulative difference in growth between high- and low-flow riffles would result in a deficit of 13 mm or 3.1 g for a 71 mm dace. The fitness consequences of such a growth deficit could include delayed maturity (Hutchings 1993), decreased reproductive success (e.g., from reduced fecundity of smaller females; Falke et al. 2010), or reduced overwinter survival (Quinn and Peterson 1996; Boss and Richardson 2002), as well as increased vulnerability to predators (Scharf et al. 2000), with potential population-level consequences.

Using mesocosms, Schaefer (2001) demonstrated that movement of a riffle-dwelling herbivore into pools during low flow was delayed by the presence of caged predators. The lack of any general increase in Nooksack dace abundance in most pools at low flows may have been due to the presence of aquatic predators, or Nooksack dace may have immigrated into pools but experienced low survival. Alternatively, Nooksack dace remaining in shrinking riffles may have been exposed to terrestrial predators (Power 1987). The point at which pool habitats confer a survival benefit for Nooksack dace likely depends on the abundance of terrestrial and aquatic predators and the relative availability of prey in pools and riffles.

Although we did not observe a general increase in density or abundance in pools with declining flow, one anomalous pool exhibited a dense aggregation of Nooksack dace. This pool was in a reach that frequently changes course during high winter flows, resulting in a channel that is braided and unstable, but has high-quality unembedded substrate that supports high densities of dace. Exposed gravel bars at this site prior to sampling indicated that seasonal reduction in riffle habitat may have already occurred before the first sampling. Dense aggregations of dace may reflect this disproportionate habitat loss, as well as the attributes of this particular pool, which was the deepest in the reach with abundant unembedded cobble, large boulder rip-rap, and the potential for upwelling hyporheic flow. Year-to-year consistency with which Nooksack dace used this particular pool could not be evaluated, as winter scour had shifted flows to the other side of the channel the following year. Dace in this and other pools in Bertrand Creek at extreme summer low flow have been observed schooling, as well as drift-feeding in the water column in stratified schools of juvenile salmonids with dace closest to the stream bed (J. Rosenfeld, personal observations). This suggests that seasonal habitat loss may cause dace to alter their normal foraging and aggregation behavior, possibly shifting to schooling aggregations in pools to minimize vulnerability to predation (Morgan and Godin 1985; Pitcher 1986). Higher densities of dace in this pool provides evidence that dace may shift to pool refugia as flows decline, but that differences among sites in hydrology, habitat quality, and fish density may cause spatial variation in flow thresholds for habitat switching.

Sublethal effects of hydrological drought can be mediated by both changes in water quality or biotic interactions (i.e., predator or prey abundance; Matthews and Marsh-Matthews 2003; Harvey et al. 2006). In experimental channels, we found that total biomass of prey taxa for Nooksack dace was significantly higher in pools than in riffles and that this pattern was largely driven by high biomass of chironomids (52%–90% of prey biomass) in pools. Although not significant, prey biomass tended to be positively related to discharge in riffles, consistent with documented responses of macroinvertebrates to drought (Minshall and Winger 1968; Matthews and Maness 1979). The importance of prey availability to growth is generally well established; however, it can be challenging to quantify the proportion of benthic invertebrate biomass that is actually available to fish. For example, although chironomids are a primary prey item for Nooksack dace (McPhail

1997), high chironomid biomass in pools did not correspond with high growth rates. A potential explanation for this is that the method used to sample benthic invertebrates in pool sediments may have included a large number of chironomids that were buried at depths inaccessible to foraging dace, thus introducing a source of sampling bias in estimates of available prey biomass in pools. Differences in the accessibility of chironomids between pool sediments and riffles may have weakened our ability to detect a relationship between growth rate and prey biomass; alternatively, some other factor may have suppressed growth in experimental pools. This highlights both the importance of accounting for biomass of prey resources, but also the availability and accessibility of benthic prey.

Understanding the impacts of hydrological drought on freshwater fish, and the extent to which refuge habitats mitigate these impacts, is crucial to the conservation of freshwater fishes (Magoulick and Kobza 2003), particularly given projected increases in the frequency and intensity of hydrological drought. This study demonstrates the sensitivity of Nooksack dace to hydrological drought, with low discharge being associated with declines in sampled abundance and decreased growth rates for fish in riffles. Low growth rates and the potential for higher predation risk in pools may provide some explanation for why Nooksack dace did not appear to be generally immigrating into pools in Bertrand Creek over the range of observed flows. This supports the inference that although pool habitats may provide refugia when riffles dewater, they do not mitigate the sublethal effects of hydrological drought. Insofar as Nooksack dace are ecologically typical of small riffle-dwelling lotic invertebrates, this study shows that riffle specialists in small streams are especially vulnerable to the negative impacts of hydrological drought and highlights the importance of preserving existing riffle habitat and sufficient stream flow to maintain riffles as high-velocity rearing environments.

Acknowledgements

We are grateful for the generosity and assistance of George Feddes and family. Special thanks to Helene Boulanger, Eric Balke, Mike Champion, Dave Allen, Aija White, Tristan Slade, and numerous volunteers for their help in the lab and field. This manuscript benefited substantially from the comments of E.B. Taylor, R.D. Moore, and anonymous reviewers. This research was supported by grants to J.S. Richardson and J.S. Rosenfeld from the Natural Sciences and Engineering Research Council of Canada and the Canadian Wildlife Federation Endangered Species Fund, to J.S. Rosenfeld from the Fisheries and Oceans Canada Endangered Species Recovery Fund and the British Columbia Ministry of Environment, and to J.S. Rosenfeld and S. Avery-Gomm by the Habitat Trust Conservation Fund. All required permits were obtained, and The University of British Columbia and the Province of British Columbia approved animal care guidelines.

References

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In *Second International Symposium on Information Theory*, Akademiai Kiado. pp. 267–281.
- Avery-Gomm, S. 2013. Assessing the impacts of habitat type and low instream flow on growth of an endangered stream-dwelling fish, Nooksack Dace (*Rhinichthys cataractae*) [online]. M.Sc. thesis, The University of British Columbia, Vancouver, B.C., Canada. Available from <https://circle.ubc.ca/handle/2429/44408?show=full>.
- Berg, M.A., and Allen, D.M. 2007. Low flow variability in groundwater-fed streams. *Can. Water. Resour. J.* 32: 227–246. doi:10.4296/cwrj3203227.
- Binns, N.A. 1982. Habitat quality index procedures manual [online]. Wyoming Game and Fish Department Publication. Available from <https://www.science.gov/catalog/item/4f4e4af4e4b07f02db6921d2>.
- Bonamis, A. 2011. Utilization of two-stage single-pass electrofishing to estimate abundance and develop recovery-monitoring protocols for the endangered Nooksack Dace (*Rhinichthys cataractae*) in Canada [online]. M.Sc. thesis, Simon Fraser University, Burnaby, B.C., Canada. Available from http://rem-main.rem.sfu.ca/theses/BonamisAlston_2011_MRM523.pdf.

- Boss, S.M., and Richardson, J.S. 2002. Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarki*) in coastal streams. *Can. J. Fish. Aquat. Sci.* **59**(6): 1044–1053. doi:10.1139/f02-079.
- Brazo, D.C., Liston, C.R., and Anderson, R.C. 1978. Life history of the Longnose dace, *Rhinichthys cataractae*, in the surge zone of eastern Lake Michigan near Ludington, Michigan. *Trans. Am. Fish. Sci.* **107**: 550–556. doi:10.1577/1548-8659(1978)107<550:LHOTLD>2.0.CO;2.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer.
- CCREM. 1987. Appendix XV: Protocols for deriving water quality guidelines for the protection of agricultural water uses. Canadian Water Quality Guidelines. Canadian Council of Resource and Environment Ministers, Task Force on Water Quality Guidelines, Ottawa, Ontario, Canada.
- COSEWIC. 2007. COSEWIC assessment and update status report on the Nooksack Dace *Rhinichthys cataractae* sp. in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- Cowx, I.G., Young, W.O., and Hellawell, J.M. 1984. The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshw. Biol.* **14**: 165–177. doi:10.1111/j.1365-2427.1984.tb00030.x.
- Dai, A. 2012. Increasing drought under global warming in observations and models. *Nature Clim. Change.* **3**: 52–58. doi:10.1038/nclimate1633.
- Dai, A., Qian, T., Trenberth, K.E., and Milliman, J.D. 2009. Changes in continental freshwater discharge from 1948 to 2004. *J. Clim.* **22**: 2773–2792. doi:10.1175/2008JCLI2592.1.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J., and Sullivan, C.A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* **81**: 163–182. doi:10.1017/S1464793105006950.
- Environment Canada. 2002. Canadian climate normals 1971–2000: Aldergrove, B.C. [online]. Available from http://climate.weatheroffice.gc.ca/climate_normals/results_e.html?stnID=702&lang=e&dCode=1&province=BC&provBut=Search&month1=0&month2=12.
- Environment Canada. 2012. Water survey of Canada archived hydrometric data online: Bertrand Creek at international boundary (08MH152) [online]. Available from <http://www.wsc.ec.gc.ca/applications/H2O/report-eng.cfm?station=08MH152&report=daily&year=2006>.
- Falke, J.A., Bestgen, K.R., and Fausch, K.D. 2010. Streamflow reductions and habitat drying affect growth, survival and recruitment of Brassy Minnow across a Great Plains riverscape. *Trans. Am. Fish. Sci.* **139**: 1566–1583. doi:10.1577/T09-143.1.
- Gelwick, F.P. 1990. Longitudinal and temporal comparisons of riffle and pool fish assemblages in a northeastern Oklahoma ozark stream. *Copeia*, **1990**: 1072–1082. doi:10.2307/1446491.
- Golder Associates Ltd. 2005. Comprehensive groundwater modelling assignment: report to the Township of Langley. pp. 1–90.
- Grossman, G.D., and Ratajczak, R.E., Jr. 1998. Long-term patterns of microhabitat use by fish in a southern Appalachian stream from 1983 to 1992: effects of hydrologic period, season and fish length. *Ecol. Freshw. Fish.* **7**: 108–131. doi:10.1111/j.1600-0633.1998.tb00178.x.
- Hakala, J.P., and Hartman, K.J. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. *Hydrobiologia*, **515**: 203–213. doi:10.1023/B:HYDR.0000027330.12182.24.
- Harvey, B.C., and Stewart, A.J. 1991. Fish size and habitat depth relationships in headwater streams. *Oecologia*, **87**: 336–342. doi:10.1007/BF00634588.
- Harvey, B.C., Nakamoto, R.J., and White, J.L. 2006. Reduced streamflow lowers dry-season growth of rainbow trout in a small stream. *Trans. Am. Fish. Sci.* **135**: 998–1005. doi:10.1577/T05-233.1.
- Hill, J., and Grossman, G.D. 1987. Effects of subcutaneous marking on stream fishes. *Copeia*, **1987**: 492–495. doi:10.2307/1445790.
- Hodges, S.W., and Magoulick, D.D. 2011. Refuge habitats for fishes during seasonal drying in an intermittent stream: movement, survival and abundance of three minnow species. *Aquat. Sci.* **73**: 513–522. doi:10.1007/s00027-011-0206-7.
- Hutchings, J.A. 1993. Adaptive life histories effected by age-specific survival and growth rate. *Ecology*, **74**: 673–684. doi:10.2307/1940795.
- Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* **22**: 415–427. doi:10.1101/SQB.1957.022.01.039.
- Inglis, S.D., Pollard, S.M., and Rosenau, M.L. 1994. Distribution and habitat of Nooksack dace (*Rhinichthys* sp.) in Canada. *Fish and Wildlife Management*, B.C. Ministry of Environment, Lands and Parks, Surrey, B.C. Reg. Fish. Rep. 237.
- IPCC. 2007. Summary for policymakers [online]. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Edited by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Avery, M. Tignor, and H.L. Miller. Cambridge University Press, UK. pp. 1–18. Available from <http://www.ipcc.ch/pdf/assessment-report/ar4/wg1/ar4-wg1-spm.pdf>.
- Jelks, H.L., Walsh, S.J., Burkhead, N.M., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D.A., Lyons, J., Mandrak, N.E., McCormick, F., Nelson, J.S., Platania, S.P., Porter, B.A., Renaud, C.B., Schmitter-Soto, J.J., Taylor, E.B., and Warren, M.L., Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, **33**: 372–407. doi:10.1577/1548-8446-33.8.372.
- Johnston, N.T., and Slaney, P.A. 1996. Fish habitat assessment procedures. Watershed restoration technical circular No. 8, watershed restoration program. Ministry of Environment, Lands and Parks and Ministry of Forests.
- Kundzewicz, Z.W., Mata, L.J., Arnell, N.W., Doll, P., Jimenez, B., Miller, K., Oki, T., Sen, Z., and Shiklomanov, I. 2008. The implications of projected climate change for freshwater resources and their management. *Hydrol. Sci. J.* **53**: 1–3.
- Kushlan, J.A. 1976. Environmental stability and fish community diversity. *Ecology*, **57**: 821–825. doi:10.2307/1936196.
- Lake, P.S. 2003. Ecological effects of perturbation by drought in flowing waters. *Freshw. Biol.* **48**: 1161–1172. doi:10.1046/j.1365-2427.2003.01086.x.
- Lancaster, J., and Belyea, L.R. 1997. Nested hierarchies and scale-dependence of mechanisms of flow refugia use. *J. N. Am. Benthol. Soc.* **16**: 221–238. doi:10.2307/1468253.
- Light, R.W., Adler, P.H., and Arnold, D.E. 1983. Evaluation of gastric lavage for stomach analyses. *N. Am. J. Fish. Manage.* **3**: 81–85. doi:10.1577/1548-8659(1983)3<81:EOGLFS>2.0.CO;2.
- Lonzarich, D.G., and Quinn, T.P. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. *Can. J. Zool.* **73**(12): 2223–2230. doi:10.1139/z95-263.
- Lonzarich, D.G., Lonzarich, M.R., and Warren, M.L., Jr. 2000. Effects of riffle length on the short-term movement of fishes among stream pools. *Can. J. Fish. Aquat. Sci.* **57**(7): 1508–1514. doi:10.1139/f00-082.
- Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *J. Fish. Biol.* **49**: 627–642. doi:10.1111/j.1095-8649.1996.tb00060.x.
- Magoulick, D.D., and Kobza, R.M. 2003. The role of refugia for fishes during drought: a review and synthesis. *Freshw. Biol.* **48**: 1186–1198. doi:10.1046/j.1365-2427.2003.01089.x.
- Matthews, W.J., and Maness, J.D. 1979. Critical thermal maxima, oxygen tolerances and success of cyprinid fishes in a southwestern river. *Am. Midl. Nat.* **102**: 374–377. doi:10.2307/2424665.
- Matthews, W.J., and Marsh-Matthews, E. 2003. Effects of drought on fish across axes of space, time and ecological complexity. *Freshw. Biol.* **48**: 1232–1253. doi:10.1046/j.1365-2427.2003.01087.x.
- Mazerolle, M.J. 2010. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.07.
- McPhail, J.D. 1997. Status of the Nooksack Dace, *Rhinichthys* sp. in Canada. *Can. Field-Nat.* **111**: 258–262.
- Minshall, G.W., and Winger, P.V. 1968. The effect of reduction in stream flow on invertebrate drift. *Ecology*, **49**: 580–582. doi:10.2307/1934133.
- Morgan, M.J., and Godin, J.G.J. 1985. Antipredator benefits of schooling behaviour in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus*). *Z. Tierpsychol.* **70**: 236–246.
- Payne, T.R. 1994. RHABSIM: user-friendly computer model to calculate river hydraulics and aquatic habitat. In *Proceedings of the 1st International Symposium on Habitat Hydraulics*, The Norwegian Institute of Technology, Trondheim. pp. 254–260.
- Pearson, M.P. 1998. Habitat inventory and enhancement needs for the endangered Salish sucker (*Catostomus* sp.) and Nooksack dace (*Rhinichthys* sp.). Fisheries Project Report No. 76A, British Columbia Ministry of Fisheries.
- Pearson, M.P. 1999. The biology and management of the Salish sucker and Nooksack dace. In *Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk*, Kamloops, B.C., 15–19 February 1999.
- Pearson, M.P. 2004. The ecology, status and recovery prospects of Nooksack dace (*Rhinichthys cataractae* ssp.) and Salish sucker (*Catostomus* sp.) in Canada [online]. Ph.D. thesis, The University of British Columbia, Vancouver, Canada. Available from <http://circle.ubc.ca/handle/2429/16110>.
- Pearson, M.P. 2009. Guidelines for the collection of Nooksack dace (*Rhinichthys cataractae* spp.) [online]. Prepared for the non-game freshwater fishes recovery team (BC). Available from <http://www.sccp.ca/sites/default/files/species-habitat/documents/Guidelines%20for%20the%20Collection%20of%20Nooksack%20Dace.pdf>.
- Pearson, M.P., Hatfield, T., McPhail, J.D., Richardson, J.S., Rosenfeld, J.S., Schreier, H., Schluter, D., Snee, D.J., Stejpovic, M., Taylor, E.B., and Wood, P.M. 2008. Recovery Strategy for the Nooksack Dace (*Rhinichthys cataractae*) in Canada. Species At Risk Act Recovery Strategy Series, Fisheries and Oceans Canada, Vancouver, B.C., Canada.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and the R Development Core Team. 2009. nlme: linear and nonlinear mixed effects models. R package version 3.1-96.
- Pitcher, T.J. 1986. Functions of shoaling behaviour in teleosts. In *The behaviour of teleost fishes*. Edited by T.J. Pitcher. Croom Helm, Sydney, Australia. pp. 294–337.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E., and Stromberg, J.C. 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience*, **47**: 769–784. doi:10.2307/1313099.
- Postel, S., and Richter, B. 2003. Rivers for life: managing water for people and nature. Island Press, Washington, D.C.
- Power, M.E. 1984. Depth distributions of Armored Catfish: predator-induced resource avoidance? *Ecology*, **65**: 523–528. doi:10.2307/1941414.

- Power, M.E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. In *Predation: direct and indirect impacts on aquatic communities*. Edited by W.C. Kerfoot and A. Sih. University Press of New England, Hanover, N.H. pp. 333–351.
- Power, M.E., Matthews, W.J., and Stewart, A.J. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology*, **66**: 1448–1456. doi:10.2307/1938007.
- Quinn, T.P., and Peterson, N.P. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Can. J. Fish. Aquat. Sci.* **53**(7): 1555–1564. doi:10.1139/f96-0925.
- R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ricciardi, A., and Rasmussen, J.B. 1999. Extinction rates of North American freshwater fauna. *Conserv. Biol.* **13**: 1220–1222. doi:10.1046/j.1523-1739.1999.98380.x.
- Rose, K.A. 2000. Why are quantitative relationships between environmental quality and fish populations so elusive? *Ecol. Appl.* **10**: 367–385. doi:10.1890/1051-0761(2000)010[0367:WAQRBE]2.0.CO;2.
- Rosenfeld, J., Porter, M., and Parkinson, E. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **57**(7): 766–774. doi:10.1139/f00-010.
- Schaefer, J. 2001. Riffles as barriers to interpool movement by three cyprinids (*Notropis boops*, *Campostoma anomalum*, and *Cyprinella venusta*). *Freshw. Biol.* **46**: 379–388. doi:10.1046/j.1365-2427.2001.00685.x.
- Scharf, F.S., Juanes, F., and Rountree, R.A. 2000. Predator size – prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Prog. Ser.* **208**: 229–248. doi:10.3354/meps208229.
- Schnute, J. 1983. A new approach to estimating populations by the removal method. *Can. J. Fish. Aquat. Sci.* **40**(12): 2153–2169. doi:10.1139/f83-250.
- Scruton, D.A., Heggenes, J., Valentin, S., Harby, A., and Bakken, H. 1998. Field sampling design and spatial scale in habitat-hydraulic modelling: comparison of three models. *Fish. Manage. Ecol.* **5**: 225–240. doi:10.1046/j.1365-2400.1998.00098.x.
- Smakhtin, V.U. 2001. Low flow hydrology: a review. *J. Hydrol.* **240**: 147–186. doi:10.1016/S0022-1694(00)00340-1.
- Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.* **60**: 1129–1157.
- Symonds, M.R., and Moussalli, A. 2011. A brief guide to model selection, multi-model inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* **65**: 13–21. doi:10.1007/s00265-010-1037-6.
- Tramer, E.J. 1977. Catastrophic mortality of stream fishes trapped in shrinking pools. *Am. Midl. Nat.* **97**: 469–478. doi:10.2307/2425110.
- USGS. 2012. Daily Data USGS 12212390 Bertrand Creek at International Boundary. United States Geological Survey, National Water Information System: Web Interface. Available from http://waterdata.usgs.gov/wa/nwis/uw/?site_no=12212390.
- Vörösmarty, C.J., Green, P., Salisbury, J., and Lammers, R.B. 2000. Global Water Resources: vulnerability from climate change and population growth. *Science*, **289**:284–288. doi:10.1126/science.289.5477.284.
- Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Reidy Liermann, C., and Davies, P.M. 2010. Global threats to human water security and river biodiversity. *Nature*, **467**: 555–561. doi:10.1038/nature09440.
- Williams, J.E., Johnson, J.E., Hendrickson, D.A., Contreras-Balderas, S., Williams, J.D., Navarro-Mendoza, M., McAllister, D.E., and Deacon, J.E. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries*, **14**: 2–20. doi:10.1577/1548-8446(1989)014<0002:FONAET>2.0.CO;2.
- Wisner, D.A., and Christie, A.E. 1987. Temperature relationships of Great Lakes fishes: a data compilation. Special Publication No. 87-3. Great Lakes Fisheries Commission.
- Xenopoulos, M.A., Lodge, D.M., Alcamo, A., Märker, M., Shulze, K., and Van Vuuren, D.P. 2005. Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Glob. Change Biol.* **11**: 1557–1564. doi:10.1111/j.1365-2486.2005.001008.x.

Appendix A

Efficiency of single-pass electrofishing

Best management practices for electrofishing of endangered Nooksack dace recommend estimating abundance from a single pass to minimize potential lethal and sublethal effects (Pearson 2009). However, the number of fish caught with single-pass electrofishing can only serve as a relative index of absolute abundance. To estimate abundance, capture efficiency must be known. A previous study by Bonamis (2011) describes a two-stage sampling

process that combined single-pass electrofishing with a 2-day mark–recapture method that may be used to assess capture efficiency of single-pass electrofishing. That method, when applied to Nooksack dace in Bertrand Creek, generated a mean capture efficiency of $28\% \pm 3\%$ (Bonamis 2011). Unfortunately, that capture efficiency could not be directly applied to our field survey because of two key differences thought to influence capture efficiency: sampling method and sampling conditions. In the present study, each riffle habitat was isolated using a stop-net at the upstream end and a modified Fyke net, with a cod-end bucket, at the downstream end (see online Supplementary Material, Fig. S2¹). Each riffle was electrofished using a single sweeping downstream pass towards the Fyke net. Stunned fish were collected with a dip net, while stunned Nooksack dace and those swimming downstream to escape the electrical field were swept downstream by fast-flowing currents and collected in the cod-end bucket. In comparison, Bonamis (2011) sampled Nooksack dace using a pole seine across a portion of the downstream channel width and electrofished the habitat in a single sweeping upstream pass. As a result, capture success with the latter method relied more on actively sighting and catching stunned fish — although it had the advantage of being less time-consuming and potentially more cost-effective in situations where the objective is general population monitoring. Additionally, the Bonamis (2011) study focused on riffle habitats with a mean (\pm SD) depth of 0.16 ± 0.19 m and velocities of 0.40 ± 0.19 m·s⁻¹, whereas the present study involved sampling habitats across a range of moderate to low discharges (0.113 to 0.007 m³·s⁻¹) and thus a broader range of depths and velocities.

We suspected that the method used in this study may have been more efficient at capturing Nooksack dace than the method employed by Bonamis (2011), particularly early in the season when higher discharges may carry stunned fish into the cod-end bucket. If so, the published 28% capture efficiency from Bonamis (2011) cannot be adopted for this study, and accounting for how changes in depth and water velocity influence capture efficiency may be important to developing accurate abundance estimates.

To explore the relationship among depth, velocity, and capture efficiency, a two-stage sampling process was conducted (Carrier et al. 2009), combining single-pass electrofishing with a 2-day mark–recapture method to estimate capture efficiency on three occasions during the summer low-flow period in 2011 (see Bonamis 2011 for description). In brief, 20–30 Nooksack dace were collected in stop-netted riffle habitats used for the mark–recapture exercise by kick-seining in a downstream direction towards the modified Fyke stop-net. Where insufficient Nooksack dace were captured in the sampling area, additional fish were collected from adjacent riffles. Fork length (mm) and mass (g) of captured fish were recorded, and each fish was marked with a small caudal fin clip. These fish were held overnight in a securely covered, perforated bucket in the stream for a 24-hour recovery period and examined for signs of stress prior to release. Healthy, marked fish were stocked evenly throughout the stop-netted riffle and allowed to acclimate and distribute themselves for 3 h before the riffle was sampled by single-pass electrofishing. All captured fish were weighed and measured, identified as recaptured or unmarked, and held in a recovery bucket before being released. Capture efficiency (%) was calculated as

$$\text{Capture efficiency (\%)} = \left(\frac{\text{recaptured Nooksack dace}}{\text{marked Nooksack dace}} \right) \times 100$$

Mean depth and velocity were measured each time capture efficiency of single-pass electrofishing was assessed (Table A1). A mul-

Table A1. Capture efficiency data collected between 22 June 2011 and 19 August 2011, using two-stage method as described by Bonamis (2011).

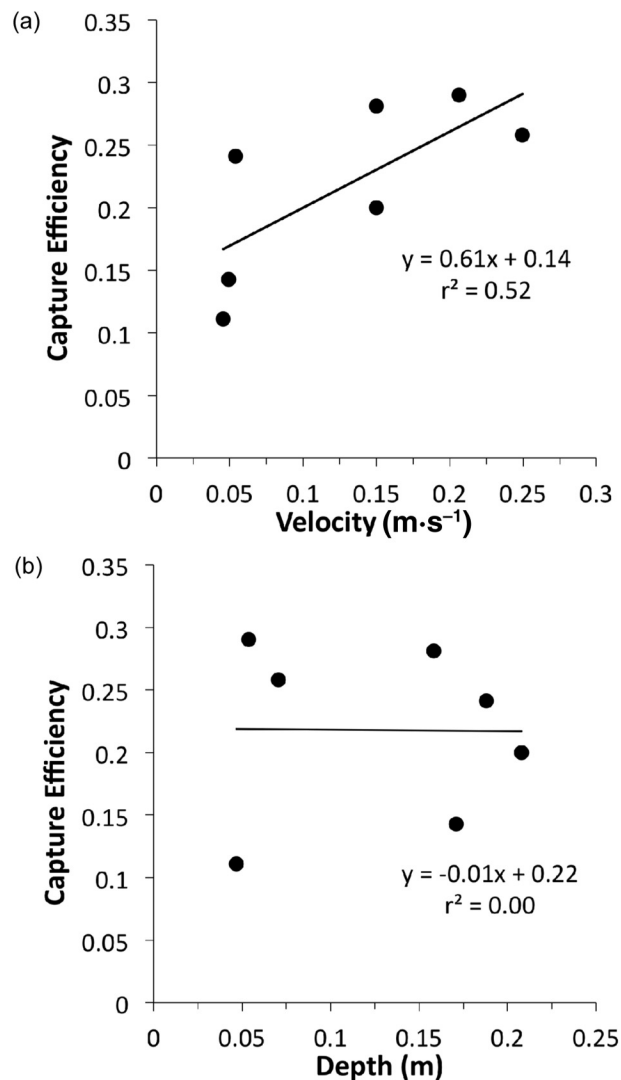
Discharge (m ³ ·s ⁻¹)	Depth (m)	Velocity (m·s ⁻¹)	Marked (M) (recaptured, R)	% Capture efficiency (R/M)
0.091	0.208±0.04	0.150±0.03	30 (6)	20.00
0.091	0.158±0.03	0.150±0.06	32 (9)	28.13
0.091	0.070±0.01	0.250±0.04	31 (8)	25.81
0.026	0.047±0.02	0.046±0.02	18 (2)	11.11
0.026	0.171±0.04	0.049±0.02	21 (3)	14.29
0.024	0.054±0.01	0.206±0.05	31 (9)	29.03
0.024	0.188±0.03	0.054±0.02	29 (7)	24.14

Note: Data are presented as means ± standard errors.

multiple regression was used to relate capture efficiency to mean habitat depth (m) and velocity (m·s⁻¹) and to test for collinearity (SPSS Version 20.0, IBM Corp., 1989, 2011). The model including both depth and velocity explained 58% of the variation in capture efficiency, but was not significant ($r^2 = 0.58$, $P > 0.05$, $n = 7$). Depth was not significant and velocity was also nonsignificant, although less so. Collinearity was not significant so depth was dropped from the model, and capture efficiency was regressed against mean water velocity (m·s⁻¹) to test for a positive relationship. The resulting model indicated that velocity had a positive relationship with capture efficiency, although this relationship was marginally insignificant ($r^2 = 0.52$, $P = 0.07$, $n = 7$). These results indicate that capture efficiency for downstream single-pass electrofishing method, combined with the modified Fyke net, tends to be higher in habitats with higher velocities and that velocity alone explains a large proportion of the variation in capture efficiency (Fig. A1). Lack of significance may be due to low statistical power, or it may indicate that there is no actual relationship between capture efficiency and velocity. We assumed the former, and the equation for the linear relationship between capture efficiency and velocity (capture efficiency (%) = $0.61 \times \text{velocity (m·s}^{-1}) \pm 0.14$) was used to calculate capture efficiencies for each of the riffle habitats where Nooksack dace were sampled. Capture efficiencies for sampled habitats in Bertrand Creek ranged from 13.9% to 36.27%. The mean (±SE) capture efficiency was $20.7\% \pm 0.7\%$, which is lower than the mean capture efficiency reported by Bonamis (2011) (28%). This difference likely related to the lower mean (±SE) velocities of habitats sampled in this study (0.11 ± 0.01 m·s⁻¹) compared with Bonamis (0.40 ± 0.19 m·s⁻¹) and to methodological differences. By using this equation to calculate capture efficiencies for each of the sampled riffles, despite the nonsignificant result, we ensure that our analyses of the effects of hydrological drought on Nooksack dace abundance and habitat use are conservative (i.e., that estimated abundance at low flows (velocities) are not underestimates associated with lower capture efficiencies).

This study suggests that the efficiency of single-pass electrofishing may be influenced by velocity and highlights the importance of considering the effects of velocity and discharge at the time of sampling on capture efficiency when estimating abundance. With benthic species, substrate size likely also affects capture efficiency, and future population studies would benefit from deter-

Fig. A1. Relationship between capture efficiency of single-pass electrofishing for Nooksack dace tended to be higher in habitats with (a) higher velocities (m·s⁻¹), but had no relationship to (b) depth (m).



mining the effect of additional habitat characteristics such as substrate on capture efficiency.

References

- Bonamis, A. 2011. Utilization of two-stage single-pass electrofishing to estimate abundance and develop recovery-monitoring protocols for the endangered Nooksack Dace (*Rhinichthys cataractae*) in Canada [online]. M.Sc. thesis, Simon Fraser University, Burnaby, Canada. Available from: http://rem-main.rem.sfu.ca/theses/BonamisAlston_2011_MRM523.pdf.
- Carrier, P., Rosenfeld, J.S., and Johnson, R.M. 2009. Dual-gear approach for calibrating electric fishing capture efficiency and abundance estimates. *Fish. Manage. Ecol.* 16: 139–146. doi:10.1111/j.1365-2409.2009.00657.x.
- Pearson, M.P. 2009. Guidelines for the collection of Nooksack Dace (*Rhinichthys cataractae* spp.) [online]. Prepared for the non-game freshwater fishes recovery team (BC). Available from: <http://www.sccp.ca/sites/default/files/species-habitat/documents/Guidelines%20for%20the%20Collection%20of%20Nooksack%20Dace.pdf>.