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Citation for the published paper:

Naman, S. M., Kiffney, P., Pess, G. R., Buehrens, T. W., & Bennett, T. R. (2014). Abundance and body condition of sculpin (Cottus spp.) in a small forest stream following recolonization by juvenile coho salmon Oncorhynchus kisutch. *Rivers Research and Applications: an international journal devoted to river research and management*, 30(3), 360-371.

doi: 10.1002/rra.2643

River Research and Applications



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Abundance and body condition of sculpin (Cottus spp.) in a small forest stream following recolonization by juvenile Coho Salmon (Oncorynchus kisutch)

Journal:	River Research and Applications
Manuscript ID:	Draft
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
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Keywords:	Sculpin, Pacific salmon, recolonization, streams



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9	3	Abundance and body condition of sculpin (Cottus spp.) in a small forest stream following
10	4	recolonization by juvenile Coho Salmon Oncorhynchus kisutch
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32	Abstract	
33	Recolonization by native species following reintroduction can affect resident species through a	
34	variety of processes. We examined the effects of natural recolonization by coho salmon	
35	Oncorhynchus kisutch on sculpin (Cottus rhotus and C. gulosus), a small benthic fish, in a small	l
36	forest stream in Western Washington, USA. Provision fish passage around a small dam allowed	
37	coho access to habitat which had been inaccessible for over 100 years. We found that density (g	
38	m ⁻² and number m ⁻²) was unchanged and body condition (the slope of the relationship between	
39	length and weight) of sculpin tended to increase from before relative to a five year period	
40	following recolonization. The proportion of sculpin comprising the total fish assemblage	
41	decreased after coho colonization relative to before but remained stable for a five year period	
42	after coho reintroduction while coho density increased over five fold. Additionally, we used	
43	Akaike's Information Criteria to evaluate the relative importance of physical and biological	
44	variables to predict sculpin density in pool habitats during the initial coho recolonization period.	•
45	Physical microhabitat variables had little support for predicting sculpin density, while there was	
46	a significant support for stream temperature; cutthroat trout (O. clarki) density and year were the	e
47	most important predictors of sculpin density. Coho density was not significant in any model. Ou	ır
48	results indicate coho introduction and subsequent recolonization has to date had minimal	
49	individual or population level effects on sculpin therefore demonstrating that species	
50	reintroductions into their native range can have no measurable effect on resident organisms.	
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4	59	Introduction
5 6	60	Many species are being actively reintroduced or are recolonizing naturally into areas where they
7 8	61	were locally extirpated. In the Pacific Northwest ecoregion of the United States, recent
9 10	62	restoration effort has focused on reconnecting freshwater migration networks for species of
11 12	63	anadromous salmonids (family Salmonidae- e.g. salmon, trout, and char) many of which have
13 14	64	been federally listed as threatened or endangered under the United States Endangered Species
15	65	Act (1970; NRC, 1996). A large amount of historic spawning and rearing stream habitat is
16 17	66	currently inaccessible due to impassible barriers such as dams and culverts (Roni et al., 2002).
18 19	67	Therefore, removal or circumvention of barriers to allow fish passage and recolonization of
20 21	68	previously inaccessible habitat has emerged as an important conservation strategy that is likely to
22 23	69	increase in the future (Roni et al., 2002; Kiffney et al., 2009).
24 25	70	Species introductions and reintroductions can influence community structure and
26 27	71	function in a variety of ways (Abrams, 1996). For example, juvenile salmonids establishing new
28 29	72	populations in previously inaccessible habitats may interact with resident fishes and potentially
30	73	compete for limited resources. Juvenile coho salmon Oncorhynchus kisutch may have
31 32	74	particularly strong impacts on resident fish communities. Coho are territorial and aggressive to
33 34	75	conspecifics and other species and have a long freshwater residence period relative to other
35 36	76	juvenile anadromous salmonids (Bisson et al., 1988; Reeves et al., 1989). In contrast, there may
37 38	77	be positive effects of Pacific salmon reintroductions as anadromous species are relatively fecund,
39	78	producing large numbers of eggs which may serve as an important resource, providing energetic
40 41	79	benefits to species that consume them (Willson and Halupka, 1995). Examining the impacts of
42 43	80	fish colonization on resident biota and ecosystem processes is a critical area of research
44 45	81	regarding the biological effects of species reintroductions; unfortunately, there has been little
46 47	82	study in this area (Kiffney et al., 2009).
48 49	83	Resident fish assemblages in low order streams of the Pacific Northwest ecoregion are
50 51	84	dominated by some combination of anadromous and resident (typically coastal cutthroat trout O.
52 53	85	clarki clarki) salmonids and non game species, particularly sculpin (Cottus spp.) (Roni, 2002;
54	86	Wydoski and Whitney, 2003). Sculpin are widespread throughout the region and may be
55 56	87	numerically dominant over salmonids in some areas (Eggers et al., 1978; Reeves et al., 1998). A
57 58 59	88	large body of literature has focused on the effects of habitat and interactions on the distribution

of Salmonids in streams (Hearn, 1987; Rosenfeld *et al.*, 2000; Quinn, 2005); however, the
importance of interactions between sculpin and salmonids has received considerably less
attention. Given the continuing shift toward community level metrics for conservation and
restoration efforts (Roni, 2003; Adams and Schmetterling, 2007), further understanding of
sculpin – habitat relationships and biological interactions will likely be beneficial in prioritizing
future conservation efforts.

We explored individual and population level effects of reintroducing anadromous salmonids on a sculpin including, riffle sculpin Cottus gulosus and torrent sculpin C. rhotus (which were numerically dominant), in a small forest stream. We used data collected opportunistically as part of a larger study examining the dynamics of natural recolonization by coho salmon in a river system where an impassible dam was modified (Kiffney et al., 2009; Pess et al., 2011; Kiffney et al., 2011). The installation of a fish ladder facility at Landsburg Diversion Dam in 2003 on the upper Cedar River (see study site description in methods) provided access for anadromous salmonids to 32 km of habitat which had been inaccessible since 1900. We examined temporal trends of sculpin density, length-weight relationships (a surrogate for body condition) and the proportion of sculpin comprising the total fish assemblage before the installation of the fish ladder (2000-2001) and for five years after initial coho recolonization (2005-2009). To our knowledge this is one of the first case studies to document the potential effects of Pacific salmon colonization on resident sculpin populations.

The recolonization of coho has the potential to affect sculpin in a variety of ways. Previous research on direct sculpin-salmonid interactions has provided mixed results. Some investigators have suggested the potential for interspecific competition as sculpin and salmonids have been shown to consume similar prey (Patten, 1975; Ruetz et al., 2003; Zimmerman and Vondercek, 2006b; Zimmerman and Vondercek, 2007a). However, other evidence suggests sculpin – coho interactions may be weak as they partition resources through differences in habitat use and foraging strategies (Moyle, 1977; Glova, 1986). If resource overlap between the species is high, we may expect a negative response in sculpin populations (density) and individual condition (length-weight relationships) as a result of direct competition. Conversely, sculpin may also benefit from salmon recolonization as some studies have shown sculpin can

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consume juvenile salmonids and eggs (Patten, 1975; Quinn *et al.*, 2012) which could result in
increased densities and individual condition of sculpin.

The response of sculpin to coho recolonization may not be predictable from other systems however. Given that coho and sculpin have historically co-occurred across their native range, it is plausible to hypothesize that they have evolved respective methods to partition resources and decrease the potential for competitive interactions. However, the local extirpation of coho from Rock Creek for over 100 years complicates predictions as interactive dynamics may differ after species have experienced a period of isolation. Sinclair (1998) suggested that interspecific interactions with resident biota may be exacerbated during early stages of species introductions. This hypothesis was supported by Ward et al. (2008) who found abundance of sculpin to be a key determinate of Atlantic salmon Salmo salar survival following reintroduction above an anadromous barrier. However, a key difference in our study is that coho naturally entered Rock Creek as juveniles (Pess *et al.*, 2011) as opposed to being artificially stocked as fry (i.e. Ward et al., 2008). Coho entering Rock Creek were likely to be of sufficient size to where we hypothesized morphological and behavioral differences would minimize their interactions with sculpin during the initial period of recolonization.

To additionally examine what biological and environmental factors influenced sculpin during early stages of coho recolonization, we modeled the relationship between sculpin density in pool habitats and a variety of predictors which included biological and physical variables. Abundance of torrent and riffle sculpin has been shown to respond positively to microhabitat conditions such as substrate (Brusven and Rose, 1981; Brown, 1991), gradient and velocity (Kiffney and Roni, 2007). Additionally, predation and competition from trout has been shown to have negative effects on sculpin abundance (Ruetz, 2003; Ramirez, 2011). There are few studies, however, which have integrated abiotic and biotic correlates to examine sculpin microhabitat abundance, especially over larger spatial and temporal scales (but see Grossman et al., 2006). We used an information theoretic approach (Burnham and Anderson, 2002; Kiffney and Roni, 2007) to estimate the relative importance of abiotic vs. biotic factors in predicting sculpin density during coho colonization in pool habitats in Rock Creek from 2005-2009. We hypothesized that coho recolonization would have minimal individual and population level effects on sculpin in Rock Creek and biotic factors (potential competition with coho and trout) would be less

important in predicting sculpin abundance than physical microhabitat features or ambientenvironmental conditions such as stream temperature.

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Methods

153 Study Site

Rock Creek is a tributary to the Cedar River (the largest tributary to Lake Washington) located in the Cedar River Watershed, which is a 36,644 hectare municipal watershed managed as a conservation area by the Seattle Public Utilities (Kiffney et al., 2009). Landsburg Diversion Dam at river kilometer 35 (distance from Lake Washington) was installed in 1900 to divert drinking water to the greater Seattle area (Figure 1) and blocked upstream migration of fish until 2003 when the installation of a fish passage facility allowed anadromous and adfluvial fish, including Pacific salmon and trout, upstream migration access to 20 km of mainstem and 13 km of tributary habitat in the upper Cedar River. Rock Creek, the first major upstream tributary to the upper Cedar River and enters the mainstem 3.4 km upstream of Landsburg. Rock Creek is the only tributary in the upper Cedar River watershed with most of its drainage area accessible to salmon (Anderson et al., 2006).

Rock Creek has a rain dominated hydrograph with peak flows in winter and spring (~November to May) and low flows in summer. Due to the management of the watershed as a drinking water source for the City of Seattle and as a de facto nature reserve, habitat conditions and processes in the watershed are largely intact. In addition to torrent and riffle sculpin (Tabor et al., 2007), the fish assemblage in Rock Creek following the fish ladder installation consists of coho and low densities of Chinook salmon O. tshawytscha, cutthroat trout, as well as speckled dace *Rhinichthys osculus* and one to three species of lamprey (*Lampetra* spp.). A small number of resident rainbow trout O mykiss, which are abundant in the mainstem Cedar River have also been observed in Rock Creek.

Study Design

In summer of 2000 and 2001, fish were collected from pool habitats (n=6) in the lower

2.6 km reach of Rock Creek to establish baseline conditions for fish populations of the Cedar

River and its tributaries before the introduction of anadromous salmon above the fish ladder (see

Riley et al., 2001; Kiffney et al., 2002). In 2005-2009 fish were collected from approximately 30

pools over a period of 3-7 days in midsummer across the same 2.6 km reach of Rock Creek (Pess

et al., 2011). Only pool habitats were sampled because coho were the focal species of the study

(Pess *et al.*, 2011). An effort was made to sample a consistent set of habitat units across years;

creation resulting from changes in channel morphology from flood events or inputs of large

wood. Fish were collected by three pass electrofishing (see Pess et al., 2011 for additional

information on fish collection and processing) measured to the nearest mm (total length for

sculpin, fork length for coho and trout) and weighed to the nearest 0.1 g using an OHAUS

Scout[®] field balance. Population size was estimated using a maximum likelihood procedure

adapted to three pass electrofishing (Rosenfeld et al., 2000; Pess et al., 2011). Fish density was

determined by summing the total weight (g) or total number of fish captured in a pool habitat

unit and dividing by pool surface area (average wetted length * average wetted width).

Prior to fish collection, habitat surveys were conducted to quantify physical

characteristics of each pool habitat unit. At each pool, wetted length and width were measured

using a handheld laser rangefinder, and maximum and minimum depth (depth at pool crest) was

determined using a stadia rod. Average current velocity was quantified by measuring velocity at

three (top, middle and bottom) points of a pool using a handheld velocity meter (Table 1). We

visually estimated dominant substrate types and categorized them using the following criteria:

fines (diameter $\le 0.062 \text{ mm}$), sand (0.062 – 2 mm), gravel (2 – 64 mm), cobble (64 – 256 mm),

continuously using data loggers (HOBO[®] Pendant temperature data loggers, Onset Corporation),

and boulder (> 256 mm) (Pess et al., 2011). Stream temperature was measured using

deployed at three locations within our sampling reach.

however, a variable number of habitat units were sampled each year due to their elimination and

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Sculpin were not identified to species in the field due to logistical constraints resulting from the large effort needed to process coho, morphological similarities of torrent and riffle sculpin and the large number of sculpin captured during electrofishing (see Pess et al., 2011). A concurrent study in Rock Creek has indicated that torrent sculpin are the dominant species in pools in our study reach with riffle sculpin making up less than 3 % of the total population (T.P. Ouinn Unpublished data), results that were in agreement with earlier work (Riley et al., 2001). These finding were also supported by inspection of a subset of lethally sampled individuals from 2007 and 2009 which showed that torrent were the dominant species (S. Naman unpublished data). Statistical analysis All statistical analysis was performed using R version 2.13.1 (R Core Development Team, 2011). Data were tested for normality using a Shapiro Wilkes normality test; a $\log(n + 1)$ transformation was used when data deviated from a normal distribution. For proportion data, an Arcsine transformation was used to achieve homogeneity of variances (Zar, 1999). Pools sampled consistently from 2000-2001 to 2005-2009 (n = 6, hereby known as "before-after analysis") were analyzed separately from the full set of pools sampled from 2005-2009 (n = 17-32, hereby known as "trend analysis"). For both analyses, we used a one way analysis of variance (ANOVA) to examine differences in density and the relative proportion of sculpin comprising total fish density across years. We also used ANOVA to test for differences in the overall mean length and weight of sculpin captured in each year. To examine temporal trends in body morphology of sculpin we tested for differences among years in the slope of the length weight relationship using analysis of covariance (ANCOVA; Roni, 2002; Gray et al., 2002). The slope parameter b was estimated using linear regression of the form ln(Weight) = ln(a) + b * ln(length)

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Where *a* is the Y axis intercept and *b* is the slope of the equation. A significant difference in theslope coefficients indicated weight varied among years for sculpin of a given length.

To predict sculpin density $(g m^{-2})$ within pools in Rock Creek from 2005-2009, a set of a priori candidate models were constructed using physical (measured at the microhabitat level), environmental and biotic variables (Table 2). Physical microhabitat variables included residual pool depth (the maximum depth minus the depth at its crest), current velocity (m s^{-1}), and dominant substrate type. Coho and cutthroat trout biomass density $(g m^{-2})$ were included as biotic variables. We partitioned trout into two size classes of greater and less than 100 mm fork length. It has been suggested that these classes represent two distinct trophic groups and may be a threshold for piscivory (Raggon, 2010; Kiffney et al., 2011). We defined stream temperature as the daily mean averaged across the summer (June 1-September 31) of each year. This metric was used due to temporal gaps in temperature data (i.e. loggers were not recording consistently across all years), and it provided the most unbiased estimate of relative temperature differences among years. To account for annual variation in density, we included year as a fixed effect covariate in the model set. Because all habitat covariates were not measured in 2000 and 2001, we did not include baseline sculpin data from 2000 and 2001 in the modeling analysis.

The set of plausible candidate models were based on existing literature relevant to sculpin-habitat relationships and biological interactions, exploratory analysis (i.e., correlation matrix), and our own experience with the study system (Table 2). Due to the large number of potential explanatory covariates and to the exploratory nature of our analysis, we only considered additive, linear models and did not include any interaction or nonlinear terms in the model set. The consideration of only simple additive models also limited the size of the model set, which averted a common problem with model selection analysis of the consideration of too many models (Burnham and Anderson, 2002).

Models were evaluated using the information theoretic approach of Burnham and Anderson (2002). Candidate models were fit to the data using linear regression (Franklin *et al.*, 2000; Grossman *et al.*, 2006). The fit of each model was assessed using a bias corrected version of Akiake's Information Criterion for small sample sizes (AIC_c). AIC_c measures the amount of information loss in each candidate model, with better approximating models receiving lower AIC_c scores. Δ AIC_c values were computed for each model as Δ AIC_c = Δ AIC_{c,i} - Δ AIC_c, min,

where $\Delta AIC_{c,i}$ is the ΔAIC_c value for the *i*th model in the candidate model set and $\Delta AIC_{c,min}$ is the minimum ΔAIC_c value among the candidate models. Models were ranked according to their ΔAIC_c weight values (w_i) which range from 0 (complete information loss) to 1 (no information loss). We considered a candidate model to have substantial empirical support and report parameter estimates and coefficients if the w_i value for a given candidate model was within 10% of the model with the highest w_i value (i.e. the best fitting model) (Burnham and Anderson, 2002). We also estimated the relative importance of predictor variables within the most plausible candidate models by summing the w_i values of all models in the set where the given predictor variable occurred. The higher the sum, the more important variable *i* is relative to other variables (Burnham and Anderson, 2002). **Results** Temporal trends in density and body condition In the before-after analysis, we found no difference in sculpin biomass (g m⁻²) or numerical density (ANOVA, P > 0.6, Figure 2a and 2b) from before (2000-2001) compared to after (2005-2009) coho recolonization. In the trend analysis (full set of pools from 2005-2009), both numerical and biomass density tended to increase over time but the slope was not different from zero (P = 0.13 and 0.16 respectively, Figure 3a and 3b). The mean proportion of sculpin comprising the fish assemblage was higher in 2000 and 2001 for both biomass (Figure 4a, P < 0.001) and numerical (Figure 4b, P < 0.001) density. The decrease in the proportion of sculpin comprising total fish density was largely due to the addition of coho which increased five-fold. However, in the trend analysis, the proportion of sculpin comprising the comprising the fish assemblage did not vary from 2005-2009 for both biomass and numerical density (P > 0.2, Figure 5a and 5b).

The mean size of sculpin captured increased after coho recolonization. Sculpin were significantly shorter (P < 0.001) and lighter (P < 0.01) in 2000 and 2001 than in other years. Page 11 of 33

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Mean lengths and weights did not significantly change among years 2005-2009 (Table 3). Sculpin length-weight relationships also increased over time in Rock Creek (Table 3). Sculpin were significantly lighter for a given length in 2001 than other years (ANCOVA, P < 0.001) and the slope of the relationship increased from 2005-2009 although the trend was not significant (P> 0.20)

295 *Predicting sculpin density in pools*

296 The best approximating model included an effect of year, small and large trout, coho density and residual pool depth (Table 4) while the second ranked model did not include coho density. The 297 298 third best approximating model included an effect of mean daily temperature but was 5 times less likely than the two higher ranked models (Table 4). Year, small trout and large trout density 299 were the most important predictor variables as indicated by their relative importance values 300 (Figure 6) and were 1.2x and 2x the relative importance value of residual depth and coho density 301 302 respectively (Figure 6). Mean daily temperature was 10x less important than the most important predictors. 303

Slope coefficients for the effect of coho density and residual pool depth on sculpin biomass density were negative but not significantly different from zero in the three most plausible models (Table 5). Small and large trout densities were positively related to sculpin biomass density and were significantly different from zero in all models (P < 0.01). In the third most plausible model, mean daily temperature was negatively associated with sculpin biomass density and did not overlap zero (P = 0.07, Table 4).

- Discussion
- 313 Temporal patterns in density and body condition

The results from our study provide several lines of correlative evidence that recolonization by coho had no measurable effect on sculpin populations in Rock Creek. First, the before-after analysis revealed no change in sculpin density following coho recolonization relative to before. We recognize that the low number of pools sampled across years of the study potentially limited our power to detect effects; however, the trend analysis further supports these findings as it showed no change in numerical or biomass density of sculpin from 2005-2009 despite the increase of coho densities over fivefold. (Pess et al., 2011). The addition of coho rapidly increased total fish density, and therefore decreased the proportion of sculpin overall from before (2000-2001) to after (2005-2009) coho recolonization. However, the lack of change in the proportion of sculpin comprising the total fish assemblage in 2005-2009 provides further reinforcement to our conclusion and indicates that the sculpin population in Rock Creek remained stable during initial coho recolonization.

These results are additionally supported at the individual level as a positive trend in length-weight relationship was observed. We hypothesize that the increasing trend in individual size and length-weight relationships of sculpin likely reflect inter-annual differences in environmental conditions in Rock Creek. Increasing body condition of sculpin may be a possible response to salmon recolonization. Direct predation by sculpin on emerging coho fry (e.g. Patten, 1975) or eggs (Quinn et al., 2012), or indirect bottom up food web effects as a result of marine derived nutrient additions (Wipfli et al., 1998) are possible pathways which may lead to increased condition of sculpin as well as other benthic consumers. However, we do not hypothesize these mechanisms are operating in Rock Creek because adult coho were not spawning in Rock Creek during the study (P.M Kiffney unpublished data) and juvenile coho entering Rock Creek were typically large enough to escape potential predation from sculpin.

When combined, our results provide evidence to support the hypothesis that coho reintroduction and subsequent colonization has had minimal population and individual level effects on sculpin in Rock Creek. Our findings are especially notable when considering that during the relatively short duration of this study juvenile coho in Rock Creek approached densities comparable to other similar systems in the region with uninterrupted histories of anadromy (Pess et al., 2011). These findings are relevant in a management context as there is concern that species reintroduction into new or previously inaccessible habitat has the potential to produce negative effects on resident communities and species (e.g., Ricciardi and Simberloff,

2009) and that negative interactions with resident organisms may limit reintroduction success (Sinclair et al., 1998).

Current understanding of the biological effects of species reintroduction and recolonization on resident communities and processes is hindered in part by the lack of empirical case studies. This knowledge gap is deepened further as non-game organisms such as sculpin are often ignored or treated as background species in many studies. Investigations have thus far yielded ambiguous results. Ward et al., (2008) found evidence of negative interactions between a reintroduced population of Atlantic salmon (Salmo salar) and resident slimy sculpin (C. *cognatus*) in the Connecticut River basin which resulted in reduced survival for Atlantic salmon. In contrast, in a tangentially related study, Glova (1987) found no difference in sculpin density when comparing habitats above (allopatric cutthroat stocks) and below (sympatric cutthroat and coho) an anadromous barrier, suggesting the presence of coho did not affect sculpin at the population level.

Our results agree with the latter study and we hypothesize the lack of any measurable effect of coho recolonization on sculpin in Rock Creek was primarily due to minimal interactions between the species. This may be partly a result of resource partitioning (e.g. Schoener, 1974) and reflective of morphological and ecological differences between the species. Coho feed primarily on terrestrially derived insects falling on the surface and drifting invertebrates (Fausch, 1993) while sculpin, which lack a swim bladder, primarily forage for benthic invertebrates at the stream bottom (Moyle, 1977; Wydoski and Whitney, 2003). Given the morphological and ecological differences between the species, the lack of effect is not surprising; nevertheless, it provides important information to managers contemplating barrier removal or species reintroduction.

Additionally, it is important to place our results into a historic context. Stream fish assemblages have evolved sympatrically and likely occurred at greater densities than currently observed in the region (Lackey, 2009). With this in mind, it is intuitive that interspecific density dependence may be a less important mechanism regulating populations during initial periods of Pacific salmon reintroductions when habitats may not be saturated. In addition to the observed results with sculpin in this study, previous investigations in the Cedar River and Rock Creek have shown no evidence of negative population or individual level effects of coho recolonization

on rainbow or coastal cutthroat trout (Kiffney *et al.*, 2009; Buehrens, 2011), species shown to
have potentially high resource overlap with coho (Bisson *et al.*, 1988; Rosenfeld *et al.*, 2000).
While the potential for negative interactions due to species reintroductions remains a concern for
fish conservation and management efforts (Brenkman *et al.*, 2008), our results suggest that
interspecific interactions between reintroduced Pacific Salmon and resident fish assemblages
may be less important than other factors in limiting populations of resident species during the
early stages of reintroductions.

Predicting sculpin density in pools

Although coho density was included in two of the three best approximating models, it was not a significant predictor of sculpin density providing further support that coho had little measurable effect on sculpin. An unexpected finding from this analysis was the strong positive relationship between small and large trout and sculpin density. Other studies have demonstrated predator facilitation (when the foraging action of one predator causes prey to become more available to a predator with a different foraging mode) between benthic feeding sculpin and drift feeding trout (Douglas et al., 1994; Miyasaka and Nakano, 1999); however, these relationships may be a function of unmeasured habitat or environmental variables and controlled experiments are necessary for us to attribute this mechanism to modeled trout-sculpin associations in Rock Creek.

No physical microhabitat variables were statistically important in predicting sculpin density. Previous studies have suggested abundance of both torrent and riffle sculpin was positively associated with high gradient, high velocity habitats with intermediate substrate composition (Hawkins, 1983; Kiffney and Roni, 2007; Wydoski and Whitney, 2003). The lack of significant microhabitat variables in predicting sculpin density was consistent with other studies however. Roni (2002) found that small scale physical habitat features had little influence on sculpin densities in streams across western Washington and Oregon. The inclusion of temperature as a significant predictor suggests the importance of ambient environmental conditions in predicting temporal patterns of abundance for sculpin in Rock Creek. This result

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was supported by other findings which have related sculpin abundance to precipitation (Roni,
2002) and stream discharge or landscape variables such as drainage area (Grossman *et al.*, 2006).

An important caveat to our study was that only pool habitats were sampled. Given that many sculpin species occur at higher densities in other fast water habitat types (e.g. riffles or glides; Roni, 2002), the non-significant effects of microhabitat variables in explaining sculpin density may be attributed to not sampling across all habitat types. Despite this limitation we believe our results offer some relevance because coho densities are typically much higher in pools relative to other habitat types (Lonzarich and Quinn, 1995; Rosenfeld et al., 2000; Roni, 2002); therefore, during summer low flow conditions, pools are the habitat type in which coho are most likely to interact with sculpin and other fish species.

Given their widespread distribution, relatively high abundance, and low mobility there is clearly a need for more effort quantifying factors that influence sculpin populations and their role in aquatic food webs. In the context of anadromous salmon reintroductions, sculpin may be an important indicator for the response of resident fish assemblages or ecosystem processes. For example, our results indicate sculpin distribution in pool habitats was not likely affected by a rapid increase in juvenile coho abundance. Moreover, the increasing emphasis on community or ecosystem level approaches to management will likely place greater importance on the ecology of non-commercial species such as sculpin. Case studies, such as ours are critical to advance our understanding of this ecologically important yet understudied group of species. We recognize that due to the observational nature of our study, we are hindered in our ability to explicitly demonstrate mechanisms which may have contributed to the resilience of sculpin to Coho reintroduction. Future research should incorporate experimental approaches to gain greater understanding of explicit ecological and evolutionary factors that may influence the response of extant species or assemblages to reintroductions.

Acknowledgements

We are extremely grateful to R. Klett, K. Kloehn, E Buhle, J. Hall, J. Cram, S. Morley, K.
Macneale, P. Roni, R. Holland, M. Leirmann and V Pelekis from the Northwest Fisheries
Science Center, J. Anderson, N. Kendell, T. Jacks from the University of Washington and

1 2		
2 3 4	432	numerous undergraduate interns for invaluable field assistance. D. Shull, S. Morley, P. Roni, R.
5	433	Tabor and M. Carey provided helpful comments on earlier versions of this manuscript. M.
6 7	434	Leirmann provided statistical advice. This work was funded by the Seattle Public Utilities Ceda
8 9	435	River Anadromous Fish Commission and the Northwest Fisheries Science Center.
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3 4	633	Figure Legends
$\begin{array}{c} 5 \\ 6 \\ 7 \\ 8 \\ 9 \\ 10 \\ 11 \\ 23 \\ 14 \\ 15 \\ 16 \\ 17 \\ 18 \\ 19 \\ 20 \\ 12 \\ 23 \\ 24 \\ 25 \\ 26 \\ 27 \\ 28 \\ 29 \\ 03 \\ 13 \\ 23 \\ 34 \\ 53 \\ 6 \\ 73 \\ 39 \\ 04 \\ 14 \\ 23 \\ 44 \\ 54 \\ 6 \\ 78 \\ 9 \\ 51 \\ 53 \\ 55 \\ 57 \\ 58 \\ 58 \\ 58 \\ 58 \\ 58 \\ 58$	634 635	Figure 1. Map of Cedar River watershed from Landsburg Diversion facility to Cedar Falls. Dotted lines indicate physical barriers to anadromous migration (from Kiffney <i>et al.</i> , 2009)
	636 637 638	Figure 2. Mean biomass (a) and numerical (b) densities of sculpin in consistently sampled pool habitat (n=6) units in Rock Creek from 2000-2001 through 2005-2009. Whiskers represent the minimum and maximum density in each year.
	639 640 641	Figure 3. Mean biomass (a) and numerical (b) densities of sculpin (\pm SE) in the full set of pool habitat units (n=17-32) from 2005-2009. Whiskers represent the minimum and maximum density in each year.
	642 643 644	Figure 4. The mean relative proportion of sculpin comprising the total fish density in pools for consistently sampled set of habitat units from 2000-2001 through 2005-2009. Whiskers represent the minimum and maximum proportion in each year.
	645 646	Figure 5. The mean relative proportion of sculpin comprising the total fish density for all pools sampled 2005-2009. Whiskers represent the minimum and maximum proportion in each year.
	647 648 649	Figure 6 . Relative importance values for covariates used to predict sculpin density (g m ⁻²) in pools. Values were obtained by summing AIC weights for all models in which a given covariate occurred.
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 Table 1. Number of pools sampled and mean (± SD) values of physical microhabitat variables and fish densities measured from 2005-2009

Voor

			Year		
Variable	2005	2006	2007	2008	2009
Pools (n)	32	34	31	17	22
Residual depth (m)	0.37 (0.08)	0.31 (0.13)	0.35 (0.15)	0.34 (0.14)	0.37 (0.14)
Velocity (m s ⁻¹)	0.22 (0.15)	0.29 (0.12)	0.27 (0.23)	0.33 (0.19)	0.25 (0.20)
Temperature (°C)	10.6 (6.4)	12.6 (5.1)	13.4 (5.2)	11.7 (4.9)	12.4 (7.10)
Trout (g m^{-2})	1.65 (1.32)	0.83 (1.01)	0.22 (0.18)	0.52 (0.27)	0.79 (0.35)
Coho (g m ⁻²)	0.29 (0.25)	0.59 (0.57)	0.64 (0.56)	0.72 (0.97)	1.79 (2.91)

Table 2. *a priori* candidate models including the number of parameters (k) used to predict sculpin density in pools from 2005-2009.

Model	Form	k
Microhabitat		
Residual depth	SC = a + b(RHD)	2
Substrate	SC = a + b(SUB)	5
Residual depth, Velocity	SC = a + b(RHD) + b(VEL)	3
Residual depth, Velocity, substrate	SC = a + b(RHD) + B(VEL) + b(SUB)	7
Year	SC = a + b(year)	5
Year, Substrate	SC = a + b(year) + b(SUB)	9
Year, Residual depth	SC = a + b(year) + b(RHD)	6
Year, Residual depth, Velocity	SC = a + b(year) + b(RHD) + b(VEL)	7
Biological Interactions		
Small trout	SC = a + b(TRT)	2
Large trout	SC = a + b(LRGTRT)	2
Coho	SC = a + b(CO)	2
Year, Small trout	SC = a + b(year) + b(TRT)	6
Year, Large trout	SC = a + b(year) + b(LRGTRT)	6
Year, Coho	SC = a + b(year) + b(CO)	6
Year, Small trout, Large trout	SC = a + b(year) + b(TRT) + b(LRGTRT)	7
Year, Small trout, Coho	SC = a + b(year) + b(TRT) + b(CO)	7
Year, Large trout, Coho	SC = a + b(year) + b(LRGTRT) + b(CO)	7
Year, Small trout, Large trout, Coho	SC = a + b(year) + b(TRT) + B(LRGTRT)	
	+ b(CO)	
Physical and Biological Interactions		
Year, Small trout, Temperature	SC = a + b(year) + b(TEMP) + b(TRT)	7
Year, large trout, Temperature	SC = a + b(year) + b(TEMP) + b(TEM	,
real, large troat, remperature	b(LRGTRT)	7
Year, Coho, Temperature	SC = a + b(year) + b(TEMP) + b(CO)	7
Year, Small trout, Large trout,	bc = u + b(ycu) + b(TEMT) + b(cc)	7
Temperature	SC = a + b(year) + b(TRT) + b(LRGTRT)	
remperature	+ b(TEMP)	8
Year, Small trout, Large trout, Coho,	+ 0(1 LWI)	0
Temperature	SC = a + b(year) + b(TRT) + b(LRGTRT)	
remperature	+ b(CO) + b(TEMP)	9
Year, Small trout, Residual depth	SC = a + b(year) + b(TRT) + b(RHD)	7
Year, Large trout, Residual depth	SC = a + b(year) + b(TRT) + b(RHD) SC = a + b(year) + b(LRGTRT) + b(RHD)	7
Year, Coho, Residual depth	SC = a + b(year) + b(CO) + b(RHD) $SC = a + b(year) + b(CO) + b(RHD)$	7
Year, Small trout, Large trout,	SC = a + U(ycar) + U(CO) + U(RIID)	1
Residual depth	SC = a + b(year) + b(TRT) + b(LRGTRT)	
Residual depui	SC = a + b(year) + b(TRT) + b(LROTRT) + b(RHD)	8
Year, Small trout, Large trout, Coho	$\pm v(\mathbf{MID})$	0
Residual depth	SC = a + b(year) + b(TRT) + b(LRGTRT)	
Kesiuuai uepui		9
	+ b(CO) + b(RHD)	9

 Table 3. Number of sculpin captured each year and their mean lengths with minimum and maximum lengths in parenthesis, asterisk indicate lengths were significantly different (P < 0.001). Slope (β) and intercept (α) parameters for the relationship of total length (mm) to weight (g) in each sampling year. Equations were of the form ln(weight)= $\alpha + \beta * \ln(\text{length})$. All equations within years were highly significant (P < 0.001). An asterisk indicates a year where the slope is significantly different (P < 0.01). To illustrate the effect of changing parameters, the predicted weight (g) is shown for each year for a sculpin which is 75 millimeters long.

Year	n	Length	Slope	Intercept (±SE)	Predicted weight at 75mm	
2000	80	58 (20, 98)*				
2001	75	65 (10, 115)*	2.037*	-7.312(0.218)	4.4 g	
2005	65	73 (27, 125)	2.996	-11.325(0.086)	5.0 g	
2006	90	73 (41, 136)	3.209	-12.225(0.079)	5.1 g	
2007	205	73 (45, 151)	3.038	-11.459(0.075)	5.3 g	
2008	129	70 (43, 120)	3.067	-11.568(0.084)	5.3 g	
2009	272	70 (19, 143)	2.871	-10.738(0.058)	5.3 g	

Table 4. AIC_c scores for the highest ten ranked candidate models predicting sculpin density. Models are ranked from lowest AIC_c score (most plausible model) to highest (least plausible).

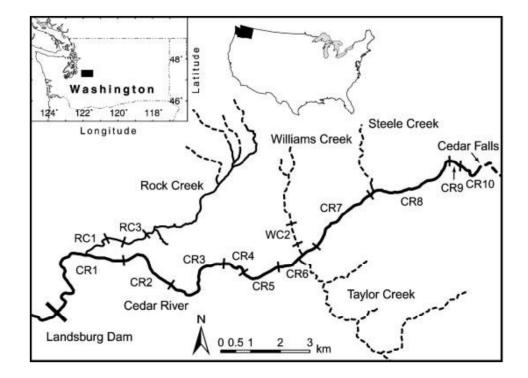
6	Model	k	AIC _c	AAIC _c	Wi
7	Year, Small trout, Large trout, Coho, Residual depth	9	982.78	0.00	0.44
8	Year, Small trout, Large trout, Residual depth	7	982.90	0.12	0.41
9	Year, Small trout, Large trout, Coho, Temperature	9	986.30	3.51	0.08
LO	Year, Small trout, Large trout, Coho	8	987.93	5.15	0.03
11	Year, Small trout Large trout	7	988.67	5.89	0.02
12	Year, Small trout, Large trout, Temperature	8	989.00	6.22	0.02
.3	Year, Large trout	6	996.04	13.26	0.00
L4	Year, Large trout, temperature	7	996.98	14.20	0.00
L5	Year, Large trout, Coho	7	997.19	14.41	0.00
.6 .7	Small trout, Large trout	3	1003.84	21.07	0.00
20 21 22					
23					
24					
25					
26					
27					
28					

River Research and Applications

35	
36	
37 38 39	Table 5. Parameter estimates (±SE) of the three highest ranked AIC models (from Table 5) with w_i values within ten percent of best fitting model. An asterisk indicates that the parameter estimate is significantly different from zero ($P < 0.05$).

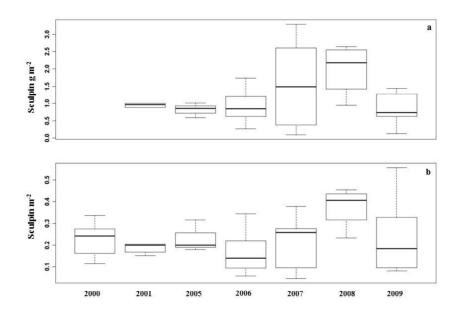
Page 27 of 33		33	River R	esearch and Applications	;				
1									
2 3	35								
3 4 5 6 7	36								
6 7		Table 5. Parameter estimates (\pm SE) of the three highest ranked AIC models (from Table 5) with w_i values within ten percent of best fitting model. An asterisk indicates that the parameter							
8 9	37 38								
10	39		ificantly different from z	-					
11 12	40								
13 14 15	41	Model Rank							
16 17	42	Parameter	1	2	3				
18 19	43	Intercept	0.132 (0.214)	0.173 (0.213)	1.689 (0.921)				
20 21	44	Year 2006	0.586 (0.192)*	0.539 (0.195)*	0.993 (0.267)*				
21 22 23	45	Year 2007	0.876 (0.199)*	0.805 (0.194)*	1.383 (0.323)*				
23 24 25	46	Year 2008	0.080 (0.224)	0.039 (0.233)	0.038 (0.245)				
26 27	47	Year 2009	0.915 (0.250)*	0.793 (0.237)*	1.290 (0.393)				
28 29	48	Small trout	0.089 (0.024)*	0.082 (0.023)*	0.088 (0.024)*				
30 31	49	Large trout	3.304 (0.616)*	3.301 (0.618)*	3.461 (0.613)*				
32 33	50	Coho	-0.088 (0.059)		-0.134 (0.061)				
34 35	51	RHD	-0.516 (0.379)	-0.061 (0.375)					
36 37	52	Temperature			-0.165 (0.086)*				
38 39	53	R^2	0.31	0.30	0.30				
40 41									
42 43									
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Naman et al. Figure 1.

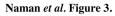


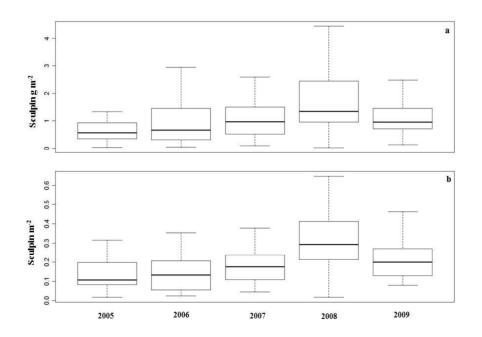
138x114mm (300 x 300 DPI)

Naman *et al.* Figure 2.



151x119mm (300 x 300 DPI)

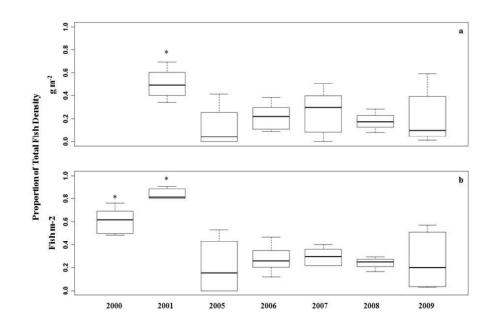




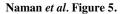
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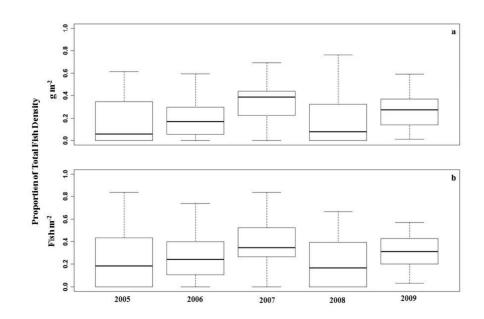
http://mc.manuscriptcentral.com/rra

Naman et al. Figure 4.

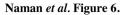


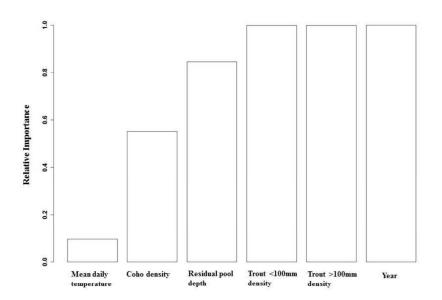
150x125mm (300 x 300 DPI)





150x125mm (300 x 300 DPI)





146x123mm (300 x 300 DPI)