Assessing freshwater life-stage vulnerability of an endangered Chinook salmon population to climate change influences on stream habitat

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ABSTRACT: We linked a set of climate, hydrology, landscape, and fish population models to estimate the relative influence of freshwater habitat variables on the abundance of a population of endangered stream-type Chinook salmon *Oncorhynchus tshawytscha* responding to a warming climate. The hydrology models estimated that increases in annual air temperature and winter precipitation would lead to increases in water temperature and changes in discharge, including higher flows during the egg-incubation period and lower flows during the summer rearing period. The spatially explicit population model estimated a resulting decline of 0 to 7 % in the number of spawners, with 3 of 4 global climate models estimating a decline of 4 to 7 %. Increased water temperature during the summer spawning period was the most limiting among habitat variables modeled, but our modeling suggested that aggressive habitat restoration (increasing forested area and reducing impervious area) could mitigate some spawner abundance reductions. Better knowledge of the links between climate changes and habitat response, including increased streambed scour due to the larger and more frequent winter high-discharge events predicted by our hydrology models, would improve our ability to estimate climate effects on populations. Future limitation by elevated summer water temperature, and potentially egg-pocket scour, would further stress an endangered population currently limited by the percentage of fine sediment around egg pockets. Identifying such changes demonstrates the utility of models that consider climate and integrate life-stage-specific habitat influences over a species' life cycle, thereby indicating restoration actions with the potential to benefit sensitive life stages.

KEY WORDS: Life-cycle model · Landscape model · Hydrology model · Downscale

1. INTRODUCTION

To effectively manage the recovery of imperiled species, there is an imperative need for understanding the cumulative effects of climate change on habi-

tat and how species respond (Groves et al. 2012, Seney et al. 2013). Each stage of a species' life history may be affected differently by changes in its habitat. For example, Radchuk et al. (2013) found positive effects from warming temperatures in all stages of an

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endangered butterfly species except survival in its overwinter larval stage, which resulted in reduced population viability and increased extinction risk. Identifying such potential bottlenecks to recovery as a consequence of forecasted climate change, by itself and in combination with other factors, is becoming an increasingly important aspect of natural resource management (Finch et al. 2014, Runge et al. 2014).

Climate change presents a challenge to Pacific salmonids because they are philopatric and have a relatively low straying rate (Neville et al. 2006, Quinn et al. 2006, Keefer & Caudill 2014). This pattern promotes local adaptation (Quinn & Dittman 1990) and may limit salmonid resilience if changes in water temperature and discharge regimes outpace their capacity to adapt. Currently, maximum water temperatures during the summer in many western USA salmon-bearing streams approach and occasionally exceed thermal preferences or tolerances of salmonids (Torgersen et al. 1999, Richter & Kolmes 2005, Goniea et al. 2006). Future increases in air temperature and changes in mountain snowpack are projected to exacerbate high water temperatures and low flows during the summer (Mote & Salathé 2010) as well as increase the frequency of high discharge events in other seasons (Warner et al. 2014), putting additional environmental stresses on fishes (Mantua et al. 2010). An understanding of these effects can ensure that habitat restoration efforts are targeted to ameliorate the anticipated negative impacts (Beechie et al. 2013, McClure et al. 2013). However, only a few population studies have analyzed life-stage-specific responses to climate change in a life-cycle context (e.g. Battin et al. 2007, Crozier et al. 2008, Radchuk et al. 2013). Important life-stage bottlenecks could be overlooked if the population-level influences of individual life-stage responses to climate change are not assessed (Dupont et al. 2010, Radchuk et al. 2013).

To better understand the potential vulnerability of an endangered salmon population, we linked a set of global climate models (GCMs) to a set of hydrology models to estimate changes in water temperature and discharge at key periods in the freshwater life stages of stream-type Chinook salmon *Oncorhynchus tshawytscha* from the Wenatchee River. We estimated the population response with a spatially ex-

Fig. 1. Diagram of links between climate, hydrology, and landscape influences on a spring-run Chinook salmon population dynamics life-cycle model, showing where factors (ovals) influencing transitions between stages of the fish life cycle (shaded rectangles) are determined by outputs of the hydrology and landscape models. Each color represents a different model

plicit life-cycle population model (Scheuerell et al. 2006, Honea et al. 2009), using the output (water temperature and flows) from the hydrology models as input, to ascertain which life stages are most influenced by the effects of climate change (Fig. 1). We focused on freshwater life stages because of our capacity to influence habitat changes there with restoration activities (Palmer et al. 2008, Bryant 2009, Yvon-Durocher et al. 2011). We examined climate effects on population dynamics for 2 habitat states as contrasting boundary conditions: a status quo (current) habitat and an approximation of historical habitat conditions (Jorgensen et al. 2009). We conducted a sensitivity analysis to determine which freshwater life stages were most vulnerable to climate change effects under each habitat condition and to assess the relative potential of different restoration actions for mitigating climate impacts.

2. MATERIALS AND METHODS

2.1. Population

Wenatchee River spring-run Chinook salmon *Oncorhynchus tshawytscha*, 1 of 3 populations that compose the endangered Upper Columbia spring-run Chinook salmon Evolutionarily Significant Unit (NMFS 1999), typically spend nearly 2 yr in freshwater after they hatch, migrate to the ocean in their second year, and return from the ocean as 4 and 5 yr old adult spawners to the river where they hatched.

Fig. 2. The study area, showing the subbasins modeled (labeled by the final 3 digits of the sixth-field hydrologic unit code) and the temperature and stream discharge stations used for calibrating the hydrology models

The Wenatchee River Basin drains about 3400 km² of the eastern slopes of the Cascade Mountains and empties into the Columbia River, the largest North American river flowing into the Pacific Ocean (Fig. 2). Wenatchee River Basin hydrology is dominated by snowmelt with the highest flows occurring between May and July and the lowest in August and September. See Jorgensen et al. (2009) for a more detailed description of the basin. We modeled all of the major salmon-producing tributaries of the Wenatchee River, including the Chiwawa, White, and Little Wenatchee rivers, as well as Nason Creek and

the upper reaches of the mainstem Wenatchee River. The Chiwawa River and Nason Creek both have fish supplementation programs producing salmon from local broodstock intended to augment the wild population. The Icicle River supports few wild Chinook salmon but is the location of a major Chinook salmon hatchery supporting commercial and recreational harvest using broodstock from fish that originated outside of the Wenatchee River Basin population.

2.2. Climate, hydrology, landscape, and population models linking climate to habitat condition and population response

We used outputs from 4 GCMs to simulate future climate scenarios. To estimate changes in stream temperature and discharge in response to potential future climate, we used air temperature and precipitation estimates from the GCMs—downscaled to 150 m, 3 h values—as inputs to a set of local hydrology models. The output of the hydrology models, water temperature and discharge, was used as input to a population model to project population response to predicted changes in climate. More details of the climate and hydrology models can be found in the Supplement at www.int-res.com/articles/suppl/c071p127_supp.pdf.

To assess the influence of climate change on salmon survival, we used a spatially explicit population model calibrated for the study area (Honea et al. 2009), using changes in mean adult spawner abundance as the population response measure. Survival through 3 freshwater stages (spawning, in-gravel egg incubation and rearing, and summer rearing) was driven by functional relationships that included water temperature (Fig. 3). Another freshwater life stage, the overwinter stage, was indirectly influenced by climate because lower discharge at the end of summer increased the number of fish moving downstream into new areas for their overwintering stage. The 3 remaining life

Fig. 3. Functional relationships incorporated in the population model that related water temperature to survival for several of the life stages, both at estimated current conditions and in the 2080s from outputs from hydrology modeling. These relationships included (a) in-gravel incubation and rearing survival (based on data from Velsen 1987 and Beacham & Murray 1989); (b) summer rearing (based on data from Brett 1952, McCormick et al. 1972, and Coutant 1973); and (c) spawner survival (based on data from Cramer 2001). Symbols represent estimates for each HUC6 subbasin that have spawning and rearing fish (Fig. 2)

stages included in the population model—juvenile outmigrants (smolts), adults in the ocean, and upstream migrating adults—occur in the mainstem Columbia or in the ocean. Although climate change will likely affect those areas as well, there is insufficient information about the projected changes in those environments and their effects on salmon. Thus, our focus was on freshwater spawning and rearing habitat where there is more information

about climate change-induced changes (Fig. 1). While we use spawner abundance as the response variable, the purpose of the model is not to predict actual spawner numbers in future climate conditions. Rather, we are comparing the relative influence of different habitat variables for which data are available, to assess which of these variables known to affect survival through different life stages is likely to have the greatest influence on future spawner abundance. Additional details of the population model are described in the Supplement (www.int-res.com/articles/suppl/m071p127_supp.pdf).

We also considered the potential for more frequent high flows during the in-gravel egg incubation and rearing stage, due to increases in precipitation (Warner et al. 2014) and more transient hydrology dominated by both rain and snow (Mantua et al. 2010), to increase streambed scour and so also egg and larval fish mortality (Lapointe et al. 2000, Goode et al. 2013). To simulate the population response to greater scour due to higher flows during the in-gravel stage, we included a scenario with a 25% increase in mortality through this stage. We did not include a functional relationship directly linking streambed scour to survival through this stage in the population model because of limited data on the relationship between flow and scour for this basin.

We estimated terrestrial habitat variables that affect fish survival through changes to in-stream habitats at the sixth-field hydrologic unit code (HUC6 hereafter; Seaber et al. 1987) subbasin unit scale using a set of landscape models developed for this basin that quantitatively link landscape attributes to fish habitat characteristics (Jorgensen et al. 2009). Landscape attributes included total forest cover, riparian forest cover, road density, stream channel slope, elevation, precipitation, and drainage area. See Jorgensen et al. (2009) for additional details of the landscape models. For this analysis, we expanded on our previous work in Jorgensen et al. (2009) by re-examining the landscape models to determine the key landscape variables that could be targets for action to ameliorate climate impacts on stream habitat. We did this by assessing which landscape variables were most frequently present in the highest-ranked models predicting climate-linked stream habitat variables—i.e. water temperature during spawning, in-gravel egg incubation and rearing, and summer rearing life stages.

Therefore, in this study, we modeled a total of 17 different combinations of habitat conditions coupled with climate scenarios. These combinations consisted of 2 extreme landscape states, climate estimated by 4

Table 1. Scenarios modeled. ‘Climate’ refers to the drivers of the water temperature and flow data used in the population model (for details on the hydrology and global climate models, see the Supplement). ‘Habitat’ refers to the landscape state influencing stream habitat condition. ‘Scour’ refers to mortality during the in-gravel egg incubation and rearing stage

Scenario name	Climate	Habitat	Scour
CurrentClimate-CurrentHabitat-CurrentScour	Current	Current	Current
Warmest-CurrentHabitat-CurrentScour	ECHAM5	Current	Current
Warmer1-CurrentHabitat-CurrentScour	CCSM3	Current	Current
Warmer2-CurrentHabitat-CurrentScour	CGCM3.1	Current	Current
Warm-CurrentHabitat-CurrentScour	PCM1	Current	Current
Warmest-HistoricalHabitat-CurrentScour	ECHAM5	Historical	Current
Warm1-HistoricalHabitat-CurrentScour	CCSM3	Historical	Current
Warm2-HistoricalHabitat-CurrentScour	CGCM3.1	Historical	Current
Warm-HistoricalHabitat-CurrentScour	PCM1	Historical	Current
Warmest-CurrentHabitat-IncreasedScour	ECHAM5	Current	+ 25 %
Warm1-CurrentHabitat-IncreasedScour	CCSM3	Current	+ 25 %
Warm2-CurrentHabitat-IncreasedScour	CGCM3.1	Current	+ 25 %
Warm-CurrentHabitat-IncreasedScour	PCM1	Current	+ 25 %
Warmest-HistoricalHabitat-IncreasedScour	ECHAM5	Historical	+ 25 %
Warm1-HistoricalHabitat-IncreasedScour	CCSM3	Historical	+ 25 %
Warm2-HistoricalHabitat-IncreasedScour	CGCM3.1	Historical	+ 25 %
Warm-HistoricalHabitat-IncreasedScour	PCM1	Historical	+ 25 %

CGMs, and an additional factor to test the hypothesis that increased scour mortality may play a significant role in determining spawner abundance (Table 1). We modeled the 2 landscape states as contrasting boundary conditions: current and historical condition. The current condition included estimates from the landscape models of the current values of habitat variables in each HUC6 subbasin. Historical conditions for the study area were estimated with the landscape models by reverting the landscape variables influenced by human development to their expected historical values. For example, forest clearcuts were reverted to fully vegetated states and roads, and other anthropogenic impervious surfaces were converted to ecoregionally appropriate land-cover classes (Jorgensen et al. 2009). For each of the 2 landscape states, current and historical, we altered the resulting habitat variables associated with climate (i.e. water temperature and flow) by the change from current to future estimated by the hydrology models starting with air temperature and precipitation output from each of the 4 GCMs. Finally, to each of these 8 scenarios (2 landscape states $\times$ 4 GCMs), we added an additional variable: a 25 % increase in mortality during the in-gravel egg incubation and rearing stage.

2.4. Life-stage vulnerability analysis

We conducted a sensitivity analysis to determine which predicted change in the habitat variables had

the greatest influence on population dynamics due to their impacts at particular life-history stages, as well as to estimate which landscape variables were most strongly associated with the influential habitat variables. We did so by running the population model, altering only one of the climate-driven habitat variables at a time while holding all other variables constant at their estimated current values and comparing the change in spawner abundance (relative to current conditions) resulting from each model run. For water temperature during the in-gravel, summer rearing, and spawner periods and for low discharge at the end of the summer rearing period, we used the hydrology model output values for each of the GCMs. In this comparison of the relative influence of variables, we also included a model run using only 25 % increased mortality during the in-gravel period to simulate the effects of increased streambed scour.

3. RESULTS

In response to habitat changes produced by the linked climate, hydrology, and landscape models (for climate and hydrology results, see the Supplement at www.int-res.com/articles/suppl/c071p127_supp.pdf), the population model forecasted either no change or a small decline in mean spawner abundance, depending on GCM. Three GCMs resulted in a 4 to 7 % decline in spawner numbers (Warmest-CurrentHabitat-CurrentScour, Warmer1-CurrentHabitat-Current

Fig. 4. Changes in wild spawner abundance (as percent change relative to estimated current numbers) resulting from scenarios of future climate under current habitat conditions, historical conditions, and to changes in individual habitat parameters in the sensitivity analysis. Increased stream-bed scour effects were simulated as a 25% increase in mortality during the in-gravel incubation and rearing period

Scour, and Warmer2-CurrentHabitat-CurrentScour in Table 1); however, Warm-CurrentHabitat-CurrentScour, which included the GCM projecting the smallest changes in air temperature, resulted in little change in spawner numbers (Fig. 4). For the 3 GCM scenarios where a decline in wild spawner abundance was observed, the spatial pattern and magnitude of the change in spawner numbers was similar, with most of the decline occurring in lower Nason Creek and the upper Wenatchee River (Fig. 5), the lowest in elevation and warmest of the major spawning areas. Historical habitat conditions with end-of-century climate conditions estimated by all GCMs resulted in an increase in mean spawner abundance of nearly 30% versus future climate at current habi-

Fig. 5. Percent contribution of each HUC6 subbasin to the decline in spawner abundance, including effects of water temperature on incubation, summer rearing, and spawning stages as well as low discharge at the end of the summer rearing stage: (a) Warm (PCM1); (b) Warmer1 (CCSM3); (c) Warmer2 (CGCM3.1); (d) Warmest (ECHAM5)

tat conditions (Fig. 4). In the modeling of landscape links to stream habitat, upland and riparian forested area and anthropogenic impervious area appeared most frequently in the highest ranked models, indicating their greater influence on stream habitat characteristics than other landscape attributes modeled. This suggests that habitat restoration may have an important role in mitigating the effects of climate change for vulnerable populations.

Fig. 6. Percent contribution of each HUC6 subbasin to the decline in spawner abundance, including Fig. 5 variables as well as 25% increase in mortality during the in-gravel egg incubation and rearing stage simulating response to increased streambed scour: (a) Warm (PCM1); (b) Warmer1 (CCSM3); (c) Warmer2 (CGCM3.1); (d) Warmest (ECHAM5)

Our sensitivity analysis, where we manipulated variables one at a time, revealed that the in-gravel egg and rearing life stage had the most influence on spawner abundance. When we reduced survival through the in-gravel stage by 25% to simulate the potential influence of increased streambed scour due to larger and more frequent high-discharge events during the in-gravel period, spawner abundance declined by an additional ~15% below numbers for the

future climate and habitat scenarios (Figs. 4 & 6). Among the life stages that had explicit habitat–survival links in our model, the one with the greatest influence on population dynamics was the spawning life stage. For all GCMs, except again Warm, end of century higher water temperature had the most substantial and negative impact on fish abundance (Fig. 4). The in-gravel and summer rearing stages responded only weakly to increased temperatures and lower summer flows, having a negligible impact on spawner abundance (Fig. 4).

4. DISCUSSION

Predicted increases in air temperature and changes in precipitation are likely to alter aspects of stream habitat that are important to salmon at different stages of their life history. Our linked climate and hydrology models showed increased mean and maximum water temperatures in all months and increased average and maximum discharge during the incubation period. There was variability, however, among the climate models regarding low summer discharge. Three GCMs (Warmest, Warmer1, and Warmer2 in Table 1) resulted in a lower mean and minimum discharge, while a more moderate GCM (Warm)—in terms of air temperature change—predicted a higher mean and minimum discharge relative to current conditions (see the supplement at www.int-res.com/articles/suppl/c071p127_supp.pdf) due to a projected increase in precipitation during the summer months.

When we linked these conditions to a population model, future climate caused small population declines, with the spawning life stage most affected by climate-driven changes in freshwater habitat (Fig. 4). Survival during the spawning stage was sensitive to changes in water temperature in the range predicted for the century's end (Fig. 3; Richter & Kolmes 2005). Predicted changes in water temperature during the in-gravel and the summer rearing stages had little influence on spawner numbers (Fig. 4). The relationship between survival and water temperature during the in-gravel and summer rearing life stages was based on multiple observational experiments for each stage (see Honea et al. 2009) and is therefore likely robust. The link between survival and water temperature at the spawning life stage, in contrast, was based on only 1 data set and should be verified as more observations are made.

We found no change in spawner abundance due to the influence of reduced summer flows on juvenile

movement downstream to overwintering habitat. The lower flows drove a greater number of juveniles to migrate downstream to reaches with more favorable flows and habitat for the overwinter period. Survival through the overwinter period was a function of the percent of cobble and boulders in downstream pool habitats, and observations indicate that availability of this type of habitat is not limiting the population (Honea et al. 2009). Therefore, when fish moved downstream as a consequence of lower flows, there was no resulting change in survival. However, more information is needed to better understand and to model survival through the overwintering stage.

With mean peak discharge during the autumn to early spring period increasing by 27 to 34 % and the current 10 yr and 100 yr peak discharge events returning with frequencies of 4–5 yr and 9–15 yr, respectively (see the supplement), increased in-gravel egg and rearing mortality due to streambed scour is likely (Lapointe et al. 2000). Although we were unable to explicitly include in-gravel mortality from scour due to a lack of basin-specific scour estimates, spawner abundance declined by 14 to 21 % below the estimates for the current climate and habitat scenario when we increased in-gravel mortality by 25 % in the future climate scenarios as a sensitivity test. These estimates of scour effects are similar to estimates of Battin et al. (2007) for Chinook salmon *Oncorhynchus tshawytscha* in a basin where rain-on-snow events between November and February are more common than in the Wenatchee River Basin. Wenatchee River Basin hydrology is currently dominated by spring snowmelt; however, if climate estimates for the end of the century hold, it may potentially change to a more transient hydrology dominated by both rain and snow (Mantua et al. 2010), likely increasing the influence of streambed scour on in-gravel mortality.

We focused our modeling on the direct effects of climate on habitat variables with links to fish survivorship through successive life stages within freshwater habitats for salmon (Moussalli & Hilborn 1986, Scheuerell et al. 2006, Honea et al. 2009). While this is an important first step in beginning to consider the effects of climate on the vulnerability of at-risk species, there are other steps that could be included in the future. For example, numerous studies have associated a diverse set of ocean condition indices to salmon ocean survival (e.g. Mantua et al. 1997, Scheuerell & Williams 2005, Zabel et al. 2006); however, at this time, the net impact on conditions for salmon survival due to forecasted changes in ocean conditions and the marine food web is difficult to

estimate (Bakun 1990, Snyder et al. 2003, Harley et al. 2006, Overland & Wang 2007, Branch et al. 2013). In addition, freshwater habitat is likely to be affected by climate change indirectly—for example, via indirect effects due to climate-induced changes in demands on water for irrigation (Donley et al. 2012) or to landscape changes, such as in vegetation patterns due to changes in precipitation, air temperature, fire regime (Flannigan et al. 2000), and insect pathogens (Dalton et al. 2013). Other considerations include climate change-induced discharge and water temperature changes that may affect interactions with other organisms, such as predators (Petersen & Kitchell 2001) or fish pathogens (Marcogliese 2001), and interactions with hatchery fish with the consequent genetic effects of interbreeding (e.g. McClure et al. 2008, Muhlfeld et al. 2014). The various potential influences not included in our study highlight the need for a better understanding of the functional forms of the relationships between habitat and survival at specific life stages and their consequences to population dynamics (Hilborn 2009).

Although we found a potential decline in Wenatchee spring Chinook salmon spawners under climate change, other regions and species may respond differently to climate change. For steelhead *Oncorhynchus mykiss*, some evidence suggests that decreasing summer discharge may be the most limiting factor in the Wenatchee River and elsewhere in the Upper Columbia River Basin (Wade et al. 2013). In contrast, in colder regions where cool water temperatures may be further below the high temperature tolerance threshold, warming may have the opposite effect and in some locations may lead to an increase in fish survival and production (Leppi et al. 2014).

Taking into account the influence of a changing climate on habitat will improve the likelihood that restoration actions will succeed in recovering at-risk species (Waples et al. 2009, Beechie et al. 2013). Our modeling found that the restoration actions that most addressed the impacts of increasing water temperature were restoring forests, both riparian and upland, toward estimated historical conditions and reducing anthropogenic impervious area. There is empirical and other modeling evidence that is consistent with these findings. For example, Pollock et al. (2009) found that the total amount of forest harvest within a basin was positively correlated with water temperature in 40 small basins in western Washington State. In the Wenatchee River Basin, Cristea & Burges (2010) used a riparian shade model linked to a stream channel heat-balance model to similarly conclude that riparian restoration would mostly offset the

effects of future warming in Nason Creek, the Icicle River, and the Wenatchee River mainstem. In another tributary of the Columbia River near the Wenatchee River Basin, Ruesch et al. (2012) used a statistical model to predict stream temperature based on flow and stream unit connectivity. They concluded that riparian restoration would partially compensate for an estimated loss of 69 to 95% of Chinook salmon habitat as a result of climate change. Elsewhere, other restoration actions may be more appropriate. For example, Battin et al. (2007) concluded that increasing habitat capacity in the lower reaches of a transitional rain and snow-melt dominated river basin by reconnecting the main channel to side-channels and to floodplain habitat would be the most effective means of mitigating changes resulting from future climate because the lower reaches had been highly modified and disconnected from their floodplains while the higher elevation reaches were mostly already protected and pristine.

While we project that water temperature during the spawning period will be more limiting by this century's end than it currently is, and that streambed scour may become more important as well, our modeling predicts that the percentage of fine sediment in gravels during the incubation period will remain the most influential freshwater habitat variable limiting spawner abundance, as we found to be the case in our earlier study (Honea et al. 2009) for present conditions. Thus, restoration priorities for freshwater habitat could remain the same, particularly because some of the same restoration actions that impact fine sediments in incubation gravels have been shown to reduce high water temperature and high discharge extremes as well. For example, reforestation and reducing riparian grazing can promote riparian forests that shade stream channels as well as reduce runoff, leading to less erosion and reduced flashiness of discharge in response to precipitation (Beschta 1997, Medina et al. 2005). Restoring riparian forests will likely be crucial to preparing streams for the impacts of climate change (Seavy et al. 2009).

5. CONCLUSION

This work demonstrates the utility of examining the impacts of habitat changes on multiple life stages to identify potential bottlenecks that may drive long-term persistence. Such models may indicate a shift in the importance of different habitat variables and life stages—as with our work indicating the increasing importance of water temperature during the summer

and perhaps high flows during winter and spring—or reveal a vulnerable life stage amid others responding positively to change—as with the overwinter larval stage in the butterfly life-cycle model investigated by Radchuk et al. (2013). Furthermore, the apparent importance of relationships about which we have little local information, such as scour and its influence on survival during the egg incubation and in-gravel rearing period, indicates worthwhile areas for further data collection and research to guide population recovery efforts.

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