DEMOGRAPHIC CHARACTERISTICS IDENTIFY SUSCEPTIBILITY OF INTRODUCED TROUT POPULATIONS TO DEPLETION BY GILLNET FOR MOUNTAIN LAKE RESTORATION

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ABSTRACT

The introduction of fish to mountain lakes has created challenges for native invertebrate assemblages and resource managers who are faced with decisions on how to deal with disturbed aquatic ecosystems. While extensive research has illuminated the physical habitats and complex food webs of mountain lake ecosystems, little is known about the self-sustaining fish populations, particularly in our study area, Waterton Lakes National Park (WLNP), Canada. We used generalized linear models to examine four population characteristics associated with the vulnerability of populations to depletion by gillnetting: 1) catch per unit effort (CPUE), 2) proportion of females, 3) proportion of mature individuals and 4) length of mature trout, as a proxy for age at maturity. There were significant differences between populations in CPUE and length of mature trout, but not in the proportion of females or mature individuals. We thus incorporated the former characteristics into a basic assessment system and ranked 11 salmonid populations by their susceptibility to eradication. The application of demographic characteristics to select introduced populations for eradication is a simple yet meaningful step in restoration commonly constrained by a lack of biological knowledge.

**KEYWORDS:** Aquatic restoration, Exotics, *Oncorhynchus clarki,* Protected areas, *Salvelinus fontinalis*

INTRODUCTION

The stocking of salmonid fishes into historically fishless mountain lakes of western North America was so widespread in the twentieth century that it created a landscape in which almost all lakes have been affected (Bahls 1992). In waters where introduced fish populations have become self-sustaining, native, fishless ecosystems have been replaced with novel systems dominated by large planktivores. If ensuing impacts are severe, resource managers may decide to restore the native ecosystems by removing introduced salmonid populations. Here, we investigate variability in demographic characteristics across introduced salmonid populations in Waterton Lakes National Park (WLNP), AB, Canada, and apply our results to restoration decisions. The goal is to rank the lakes according to their suitability for restoration based on demographic characteristics that may render them more susceptible to depletion and ultimately extinction.

Gillnetting is a viable method of eradicating trout populations in mountain lakes, though success requires multiple years of netting, substantial resources and is constrained by lake morphology (Knapp and Matthews 1998). Gillnets function by lethally entangling fish at the gills as they attempt to swim through the undetectable mesh. The successful removal of *S. fontinalis* from a small Sierra Nevada lake required 3679 net days over three years (Knapp and Matthews 1998). Five additional lakes in Sierra Nevada were restored by gillnet from 1996 to 2003 (Vredenburg 2004). The removal of the same species from Bighorn Lake in Banff required over 10,000 net nights over three years (Parker et al*.* 2001). Other trout-removal projects occurred in the Devon Lakes system in Banff National Park and an additional six lakes in Sierra Nevada, (C. Pacas, Parks Canada, pers. comm.; Knapp et al*.* 2007); both spanned multiple years. Gillnets have also been used effectively to suppress trout population density in several mountain lakes under intense netting regimes (Gresswell 2009, Rosenthal et al*.* 2012). Despite the sheer effort required, gillnetting is typically preferred over the application of piscicides such as rotenone, which have lethal affects on invertebrates and can prolong time to recovery (Anderson 1970). Gillnetting, in contrast, has little to no impact on non-target species.

Given the substantial effort required to reduce fish populations and the number of mountain lakes affected by trout introductions, a simple method of prioritizing lakes for management would facilitate restoration decisions. Indeed, ranking systems are widely used for invasive non-native plants for which numerous infestations of the same species exist, rendering management priorities, exacerbated by limited resources, difficult to assign (*e.g.* Pheloung et al*.* 1999, Skurka Darin et al*.* 2011). Knapp and Matthews reported that success of gillnetting in mountain lakes is dependent on lake depth, surface area, outlet width and area of stream spawning habitat (1998). Though the biota of mountain lakes remains relatively unstudied, physical morphometric characteristics are usually known. Hence, we are interested in quantifying trout biology characteristics that influence the susceptibility of populations to over-exploitation by gill net.

Conservation theory suggests that certain demographic characteristics increase a population’s extinction risk, specifically population size, proportion of breeding females, age-at-maturity, and body size at maturity. These characteristics can be reversed to identify exotic populations vulnerable to depletion. First, as the effect of demographic stochasticity is stronger on smaller populations (Lande 1988), population size is also negatively associated with extinction risk. Second, the proportion of females in a population has a similar association, particularly in sexually reproducing organisms where females limit reproduction rates, such as in some salmonids (Blanchfield and Ridgway 1997). Third, age-at-maturity has been used to predict extinction risk across multiple taxa (Hutchings et al*.* 2012), and is positively correlated with extinction risk in freshwater fishes (Anderson et al*.* 2011). Marschall and Crowder (1996) found that average size and age-at-maturity affected brook trout population viability; populations reacted most negatively to factors that decreased the survival of large juveniles and small adults, and removing large mature individuals was not necessarily detrimental to the persistence of the population because brook trout can reproduce at a small size (1996). Finally, body size is also a factor in the efficiency of gillnets, since catchability generally increases with fish size (Jensen 1995, Finstad et al*.* 2010, Borgstrøm et al*.* 2012). Individuals that mature at a large body size are thus easier to remove than individuals that mature at a smaller body size.

We therefore examined variation in population density (in lieu of population estimates), the proportion of females and mature individuals in the population, and the length of mature individuals, as a proxy for age-at-maturity, across 11 previously stocked lakes in WLNP. We assumed that trout populations that are characterized by low density, few females, few mature individuals, and a large body size at maturation, would be more amenable to eradication by gillnet.

MATERIALS AND METHODS

Study Site

WLNP (49.0458**°**N, 113.9153**°**W) protects 505 km2 of the southern Canadian Rockies. The weather is characteristic of mountain environments; the average snowfall is 481.5cm per year and an average of 192 days per year have a minimum temperature above 0°C. WLNP contains 22 high elevation lakes that range from 1524m to 2195m asl. Previously fishless, stocking by the park commenced in the 1920s and ended in the 1980s, during which *Salvelinus fontinalis, Oncorhynchus clarki,* and *Oncorhynchus mykiss,* were introduced. Thirteen lakes presently retain trout populations that have become self-reproducing, 11 of which were included in this study (Table 1). Two lakes were excluded because they could not accurately be sampled using the same methods due to their uncharacteristically larger size.

Data Collection

*Trout populations -* Trout populations in twelve mountain lakes were sampled, but two lakes were confirmed fishless. All lakes were sampled twice in the ice-free season, between July and September 2011, except for Crypt lake (CT), which was sampled in July and August 2012. Spring sampling occurred between June and July, summer sampling occurred in July and August. Multiple visits were made to quantify seasonal variation.

Between one and five monofilament gillnets were set in each lake depending on lake size (manufactured by Lundgrens Fiskredskapsfabrik AB, Stockholm, Sweden). The overnight bottom sets optimized periods of high trout activity and we aimed for a consistent net duration of 14 hours. Nets were 30m long, with five 6m panels of different mesh gauge (18.5mm, 25.0mm, 38.0mm, 43.0mm and 55.0mm), arranged sequentially. The nets were set perpendicular to the shoreline, with one end secured to a fixed feature on shore and the deep end anchored to the substrate. The orientation of the smallest mesh was alternated equally between lake-end and shore-end to reduce bias towards fish size. Nets were spaced evenly around the perimeter of the lake and all shoreline types were covered as best as possible. Locations were marked using GPS.

In the morning, nets were collected from an inflatable raft. Fish were measured to the nearest millimetre, weighed to the nearest gram, identified to species, and assessed for sex and maturity. Sex and maturity were determined by dissecting each fish and observing gonads. Each fish was assigned a unique number; the corresponding mesh size and net was recorded. A subsample of the catch representing the range of sizes caught was sampled for stomach contents and age determination.

Statistical Analyses

We used generalized linear models (GLMs) to assess variation in the four demographic characteristics (density, length of mature individuals, proportion of females and proportion of mature individuals) across populations. The characteristics were calculated for each net, so each lake was represented by multiple datapoints. Catch per unit effort (CPUE) was used as a proxy for density and calculated as a ratio of number of individuals caught to duration of net set. Fork length of mature trout, a proxy for age-at-maturity, was the mean fork length of only the mature fish in the catch. Proportions were calculated as the number of female individuals and mature individuals divided by the total catch per net. CPUE and length data were normally distributed hence were modeled with a Gaussian distribution. Data for the proportion metrics were not normally distributed, so a binomial distribution was applied, weighted with the number of fish caught. Explanatory variables other than population included in the model were fish species, sampling period, and their interaction. The Akaike Information Criterion (AIC, Akaike 1973) was used to select among the ten models for each demographic characteristic; the lowest AIC value represents the most parsimonious model and models within 2 ΔAIC were ordered by the number of variables (Burnham and Anderson 2002). All statistical analyses were performed in R Statistical Software (R Statistical Software, R Development Core Team).

Ranking Lakes for Trout Eradication

We used the above analysis of demographic characteristics to indicate suitable factors on which to rank populations for removal. Lakes were ranked from one to eleven for each characteristic applied, where one represents the condition of the population that is most amenable to eradication. Scores for each characteristic were summed for each lake, yielding a final ranking of lakes by their suitability for restoration.

RESULTS

Fifty nets were set in 12 lakes in 2011, plus an additional eight nets in the remaining lake (CT) in 2012. A total of 1369 trout were caught in ten of the lakes sampled. Two lakes yielded no fish. Three species were represented: *O. clarki, S. fontinalis*, and *O. mykiss*. All lakes contained exclusively either *O. clarki* or *S. fontinalis*, except Little Akamina Lake, in which a small number of *O. mykiss* were caught. No further analysis was done on this species. A combined total of 706 *S. fontinalis* were caught in CR, TU, TL and AK, while 649 *O. clarki* were caught in LN, LH, CL, AL, GO, LO and CT (lake acronyms defined in Table 1). Gillnetting confirmed an absence of fish in LS and CU.

Demographic Characteristics of Trout Populations

We found that population was the most important variable explaining the variation in two demographic characteristics: CPUE and fork length of mature fish. For the GLMs based on CPUE data, the best-fit model included population and season and explained 83% of the variability in the dataset (Table 1; linear regression, r2 = 0.83, F11,46 = 19.97, *p* < 0.001). Removing the season variable revealed that the variation across populations was far more important than that across seasons (linear regression, r2 = 0.77, F10,47 = 15.43, *p* < 0.005). CPUE was consistently higher in the spring than in the summer (Figure 1a). When averaged over season, CPUE ranged from 0.63 (LH) to 1.71 (CL), except in two lakes where CPUE was much higher (TU=2.49, TL=2.59; Figure 1a). Correlation analysis showed that CPUE was not affected by variable set durations (r(52) = 0.060, t = 0.45, *p* = 0.7).

The model that best explained fork length of mature trout included only population as an explanatory variable (Table 1; linear regression, r2 = 0.81, F10,47, p < 0.001). Average values were distributed evenly across a range of 195.2mm (TU) to 292.2 (LN), but mature trout were far larger in CT (327.4mm; Figure 1b).

Variation across population was not evident in the remaining two demographic characteristics: the proportion of females and the proportion of mature trout (Table 2 and Figures 1c and d). GLMs revealed that the best model for both characteristics was the null model, indicating that variation was also not evident across season or species (Table 2).

*Ranking Lakes for Trout Eradication*

Our ranking system identified two lakes, Lineham Hourglass (LH) and North Lineham (LN), as the most suitable for trout eradication by gillnet (Table 3). The evaluation employed CPUE and length of mature individuals at equal weights, as our GLMs suggested that population had a similarly strong influence on both. We excluded the proportion of females and mature individuals from the assessment because we found no evidence of significant variation across populations (Table 2). AL, LO, CT, CR and AK were the next highest-ranked lakes, followed by CL and GO. TU and TL were by far, the least appropriate lake for restoration by trout removal (Table 3).

DISCUSSION

Demographic Characteristics of Trout Populations

Our results indicated that variation in two demographic characteristics (CPUE and fork length of mature individuals) of WLNP trout populations was explained by population-level differences. These characteristics are therefore pertinent to the selection of introduced populations for removal in the event of lake restoration.

The finding that CPUE and fork length at maturity varied across populations was not unexpected given the substantial variation in lake morphometry, chemistry, and food web composition. Stocking histories and fishing use also differed from lake to lake and are further sources of variation. Similar ranges in density (<0.1-6.8 fish hr-1 per 30.5m net) and mean lengths (11-56cm) were reported for *S. fontinalis* in 183 Rocky Mountain lakes in Wyoming, USA (Chamberlain and Hubert 1996). Lacustrine populations in the eastern, native range also demonstrated impressive variation in CPUE and mean length (Lachance and Magnan 1990, Quinn et al*.* 1994, Magnan et al*.* 2005).

The reported variation in these stocked populations was generally attributed to lake morphometrics (size and elevation of lake) and the density of other fishes (Chamberlain and Hubert 1996), while fishing intensity, the density of competitors and community complexity explained variation in density in the native range (Lachance and Magnan 1990, Quinn et al*.* 1994, Magnan et al*.* 2005). Growth rate of Alberta populations was related to amphipod abundance, productivity, and water temperature and negatively related to elevation (Donald et al*.* 1980). Variation in the eastern distribution was explained by competitor biomass, community complexity, salmonid diversity and fishing intensity (Lachance and Magnan 1990, Quinn et al*.* 1994, Magnan et al*.* 2005).

*O. clarki* populations display similar variation in CPUE and body length, but perhaps for different reasons. In the Bighorn Mountains of Wyoming, mean total length ranged from 220-425mm and density from 0.4-2.4 fish net-1 hour-1, across 19 lakes (Bailey and Hubert 2003). Unlike *S. fontinalis, O. clarki* mean length was not associated with environmental factors but with density and lake accessibility (Bailey and Hubert 2003). Meanwhile, accessibility was the only factor associated with CPUE. In the absence of further studies on lake populations, spatial variability in size at maturity was observed *O. clarki* in Montana streams (110mm to 180mm; Downs et al*.* 1997). Overall, the demographic characteristics of density and length, of both *S. fontinalis* (in novel and native habitats) and *O. clarki,* are spatially variable due to physical and chemical lake attributes, food web composition, fishing intensity and the density of other fishes.

Though population explained most of the variation in WLNP trout density, season also had an effect. Densities were consistently lower in the summer, which could be due to decreased activity in the littoral zone during the later sampling period. During the period of summer stratification, *O. clarki* reportedly avoid near-surface waters but are nearer to the surface when lakes are mixed (spring and fall) (Nowak and Quinn, 2002, Baldwin et al. 2002). A similar trend in WNLP’s dimictic lakes could be expected to reduce the efficiency of shoreline gillnet sets in the summer. Densities could also have been reduced by efficient gillnetting in the spring sampling period, leaving reduced numbers of trout vulnerable to gillnets in the summer.

The proportion of females or of mature individuals did not vary across populations. Rather, our results suggested a high amount of variability within each lake, particularly for the proportion of females (Figure 1c). Though the mean values for both species were comparable to reports by Downs et al*.* (1997) and Meyer et al*.* (2003), they do not describe the variation within each lake. Despite literature support for these factors weighing heavily on extinction risk due to female-limited reproductive strategies (Blanchfield and Ridgway 1997), we did not find the proportion of females or of mature individuals to be useful in predicting population decline. These factors were thus omitted from our ranking of populations for depletion.

Management Implications

For aforementioned reasons, only trout density and fork length of mature trout were used in a ranking system to distinguish populations with higher susceptibility to population depletion by gillnet. Similar assessment tools have been principally developed for invasive land plants, where ecological gains can be optimized by prioritizing populations for management action (*e.g.* Pheloung et al*.* 1999, Skurka Darin et al*.* 2011). The management of freshwater fishes has also recently benefited from modifications of such tools to aquatic invaders. For example, Copp et al. (2009) developed the Fish Invasiveness Scoring Kit (FISK) to distinguish potentially invasive and non-invasive species, which was used as a pre-assessment for the more instructive modular assessment tool by Britton et al*.* (2011). The latter incorporates species prioritization, population-level risk to receiving waters, management action impacts and costs of management actions, to assess introduced fish populations for management priority. Such systems are effective because they can be molded to fit the values of a particular region while retaining the structure needed to maintain transparent decision-making in governmental organizations. Even within the umbrella of national mandates, regions may value resources differently (*e.g.* angling value) and managers can assign higher weight to the criteria that have greater importance in their particular jurisdiction. A downfall to the majority of ranking systems is that they are impact-based, which is impractical in situations where impacts are equal across the landscape, such as WLNP. Fine-tuning existing assessment tools to hone in on demographic differences that affect management action success will improve their practicality in these landscapes.

We were able to identify demographic characteristics that varied across introduced trout populations in WLNP, and to apply them to indicate populations that are most susceptible to eradication. Our cursory ranking system specifically identified Lineham Hourglass Lake (LH) and North Lineham Lake (LN) as top candidates for trout depletion, based on demographic characteristics that had not previously been measured in WLNP. These lakes have a similar combination high density and low size of mature trout. They also represent similar points on environmental gradients including elevation, lake depth, lake area and accessibility. Though these lakes may contain the best populations to deplete base on biological characteristics, they are remote and difficult to access by foot and helicopter. The safest route to access LH and LN is via an 8km trail over a ridge, followed by a few kilometres of steep off-trail terrain. Unsurprisingly, these lakes receive low visitor use and fishing pressure, but are highly valued as representations of undisturbed ecosystems. Thus, further manipulation of the Lineham Lakes basin may be opposed by conservationists and backcountry users. Nevertheless, the results suggest that human and physical considerations could supersede biological factors when selecting lakes for restoration. The responsibility of resource managers to uphold regional values when making management decisions is facilitated by ranking systems such as that presented in this study, and by the provision of hard-to-measure biological data.

Ironically, this study concurrently instructs trout eradication and conservation. That is, we have found support of intraspecific diversity in exotic populations, which can be considered as biodiversity (Fraser and Bernatchez, 2001), particularly in western North American freshwater habitats depauperate of native fish fauna (Keeley et al*.* 2005). If restoration is not pursued, the population characteristics investigated in this study are still valuable for the management and continued monitoring of high mountain lakes.

**Table 1.** Characteristics of study lakes in WLNP, physical characterstic data from Anderson 1975. Chemical characteristics are SC=Specific Conductivity, TDS=Total Dissolved Solids and pH. Watershed acronyms are CL=Cameron Lake, CC=Cameron Creek, UWL=Upper Waterton Lake, BB=Blakiston Brook, BC=Bauerman Creek WBC = West Boundary Creek.



**Table 2**. Results of two factor generalized linear models (GLMs) to assess the importance of population, season, species and the interaction of season and species on the variability of four demographic characteristics (CPUE, fork length of mature individuals, proportion of females and proportion of immature individuals).



**Table 3**. Ranking of 11 previously stocked WLNP lakes by susceptibility, based on demographic characteristics CPUE and fork length of mature trout (FLM). Lake codes as per Table 1.



**Figure 1.** Mean values (± standard error, SE) of four demographic characteristics for eleven trout populations in WLNP. Lake codes as per Table 1. Dark grey bars represent spring data, light grey bars represent summer data. Dashed line divides *S. fontinalis* (left) from *O. clarki* (right). Only one net was cast in the spring in LN, so standard error could not be calculated.

a)

b)

d)

c)

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