Do native species limit survival of reintroduced Atlantic salmon in historic rearing streams?

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ABSTRACT

Reintroduction of extirpated populations creates a unique context that can exacerbate the effects of interactions among species. Thus, reintroduced populations may be particularly vulnerable to predators and competitors, including native species with which they historically coexisted. In this study, we evaluated the effect of native fishes on survival of reintroduced Atlantic salmon (*Salmo salar*) in the Connecticut River basin, where the native salmon population is extinct. Juvenile salmon are stocked annually in many Connecticut River tributaries. We sampled salmon reintroduction sites across tributaries with different fish communities to determine whether native fish reduce the success of salmon reintroductions (N = 19 site-years). Increased density of slimy sculpin (*Cottus cognatus*), a native generalist predator, was associated with reduced recruitment of reintroduced salmon. Salmon first-summer survival declined with increased sculpin density across sites, and low first-summer survival led to reduced densities of overyearling salmon the subsequent year. Hierarchical partitioning analysis showed that the negative relationship between sculpin and salmon was independent of potentially confounding variation in other fish community or habitat characteristics. Negative effects of native, historically-sympatric species, particularly generalist predators, can impede restoration of extirpated populations.

1. Introduction

As the number of local extinctions increases, reintroduction of extirpated populations becomes an increasingly important tool in conservation. Unfortunately, reintroductions often fail to result in established, sustainable populations (Dodd and Seigel, 1991; Wolf et al., 1998; Fischer and Lindenmayer, 2000). Numerous studies show that interactions with exotic species can prevent the successful reestablishment of extirpated populations, as exemplified by the dramatic impacts of exotic mammalian predators on reintroduced Australian fauna (Short et al., 1992; McCallum et al., 1995; Sinclair et al., 1998). Although much less studied, reintroduced popu-

lations may also be vulnerable to the native predators and competitors with which they previously coexisted. In this study, we examined this important aspect of conservation strategy by asking whether native, historically-sympatric fish limit the survival of reintroduced Atlantic salmon (*Salmo salar*) in their historic rearing habitat in the Connecticut River basin, USA.

The unique context of reintroduction programs can exacerbate the effects of interactions between species, such that reintroduced populations are disproportionately vulnerable to predators and competitors. For example, populations reintroduced at low density are disproportionately vulnerable to common, generalist predators (Sinclair et al., 1998; Gascoigne

and Lipcius, 2004), and this susceptibility to predation may be exacerbated by the reintroduced population's lack of experience or adaptation with local predators (Griffin et al., 2000; Shier and Owings, 2006). However, experience from biological control introductions shows that the effects of predators and competitors on introduced populations are difficult to detect, even when they decimate introduced populations (Hunt-Joshi et al., 2005). Here, we tested whether native predators and competitors reduce reintroduction success by comparing the success of salmon reintroductions across a range of native fish communities.

Salmon and trout (salmonids) are culturally and economically important fishes which have experienced massive population extirpations. Nearly all salmonid species have endemic populations that are recently extinct or endangered (Williams et al., 1989; Behnke, 2002) and more than two hundred populations of anadromous salmon in North America are extinct or severely reduced (Nehlsen et al., 1991; Musick et al., 2000). Atlantic salmon in particular have been eliminated from much of their historic range in the United States, and many populations of the species are in decline worldwide (Mather et al., 1998). Restoration and recovery of Atlantic salmon and other endangered salmonids often focuses on reintroducing populations into historically-occupied habitat (Harig and Fausch, 2002; Gephard and McMenemy, 2004). Thus, identifying the factors that determine success of these reintroductions is essential for effective recovery. Enormous effort is devoted to identifying and restoring suitable habitat for salmonids (Folt et al., 1998; Mather et al., 1998; Armstrong et al., 2003). However, studies of the effects of exotic species show that the composition of the existing fish community is also influential in determining whether salmonid reintroductions are successful (Harig et al., 2000; Scott et al., 2003). Nonetheless, almost nothing is known about the role of the native fish community in determining salmonid reintroduction success. This clear knowledge gap and its likely importance to population restoration provide the rationale for our study evaluating the effect of native fish on survival of reintroduced Atlantic salmon.

Atlantic salmon were extirpated from our study system in the Connecticut River basin when dams blocked spawning migrations nearly 200 years ago. An ongoing effort to restore Atlantic salmon to the Connecticut River centers on reintroducing juvenile salmon into their historic freshwater nursery habitat in tributary streams, where they reside for 1–4 years (usually 2) before migrating to sea (Nislow et al., 2004; Kennedy et al., 2002, 2005). Although millions of salmon fry are introduced annually in tributaries throughout the Connecticut River basin, very few adults return to spawn (<0.01% of stocked fry since 1986; Gephard and McMenemy, 2004). Previous studies indicate that there is considerable unexplained variation in survival and production of reintroduced salmon across tributaries (McMenemy, 1995; Nislow et al., 2004). Thus, to evaluate the effects of native fish on reintroduced salmon, we compared survival and density of reintroduced salmon across Connecticut River tributaries with different resident fish communities.

2. Methods

2.1. The study system

Field sites were on third- and fourth-order tributaries of the upper Connecticut River in New Hampshire and Vermont, USA. All of the study sites had wooded riparian areas, although all were near access roads. Watershed land cover at all sites was predominantly forested with some residential and agricultural land use. Stream substrate at all sites was dominated by coarse gravel and cobble (other stream characteristics in Table 1).

There is no natural reproduction of salmon in the study streams. Salmon fry were scatter-stocked at known density (range: 30–80 fry per 100 m^2) throughout each stream in late April or early May as part of the ongoing Atlantic salmon restoration program. Fry were stocked before they exhausted yolk resources and started feeding, at 0.15–0.2 g. All salmon fry for this study were produced at the White River National Fish Hatchery, Bethel, VT and were the offspring of adults whose parents had returned to the Connecticut River.

The resident fish community in the study streams consisted primarily of slimy sculpin (*Cottus cognatus*), cyprinids – mostly blacknose and longnose dace (*Rhinichthys atratulus* and *R. cataractae*), and brook trout (*Salvelinus fontinalis*). Other native species were uncommon; however, one exotic species, rainbow trout (*Oncorhynchus mykiss*), was present at three sites. These fish all potentially overlap with salmon in resource and habitat use, but they generally differ in foraging behavior. Trout, like salmon, generally hold position at a defended feeding territory and feed on drifting invertebrates. Sculpins feed on many of the same taxa as salmon and trout,

	Mean	Range	r	P	Independent contribution (%)	P
Sculpin density	32 per 100 m^2	0–126	−0.68	0.01	36%	0.002
Brook trout density	4 per 100 m^2	0.1–17	0.22	–[a]	20%	0.15
Dace density	44 per 100 m^2	1–117	0.43	0.41	5%	0.76
Width	6.6 m	4–10	−0.01	–	1%	0.49
Gradient	1.9%	1.2–3.7	0.27	–	7%	0.98
Early season habitat	27%	12–42	0.67	0.01	30%	0.01

Table 1 – Summary of predictors and their relationship to first-summer salmon survival (as final density)

The independent contribution is the proportion of the explained variation in survival that can be attributed to a predictor independent of correlations with other predictors, with P-values from a randomization test. Total explained variation was 73%.

a Bonferroni-corrected P-value >1.

but from the stream bottom – they lack a swim bladder and are nearly always on or under the substrate. Dace generally forage in loose, roving schools and are omnivorous, feeding on invertebrates and benthic algae. Brook trout are known predators of juvenile Atlantic salmon (Mohler et al., 2002; Henderson and Letcher, 2003). Some studies suggest that sculpins are also important predators of salmonid fry (e.g. Gaudin, 1985).

2.2.   Field study

We conducted field work over four years: 1997, 1998, 2003, and 2004. In 1997 and 1998, we sampled six streams in the West and White River drainages, major Connecticut River tributaries in Vermont (see Nislow et al., 1999; Kennedy et al., 2004 for descriptions of these drainages); in 2003 and 2004, we sampled five sites on New Hampshire tributaries of the Connecticut River. Thus, we collected data for 22 site-year combinations. However, a major flood at three sites in 1998 severely reduced survival of young-of-the-year (YOY) salmon (Nislow et al., 2002), so we excluded those sites from analysis of YOY survival. All of our sites in the same drainage were separated by at least 2.5 km, so we assumed that movement of YOY salmon among sites within a year was negligible (Beall et al., 1994; Einum et al., 2006).

Each study site was a 100-m long stream reach representative of local stream habitat. There was no difference in habitat characteristics on the study sites and 400 m adjacent reaches (Ward, unpublished data). At each study site, we conducted three repeated habitat surveys through the spring and early summer (May–June) in the first year of sampling. For each survey, we measured stream width at five randomly placed transects and water depth and velocity at 0.5–1 m intervals across each transect. We used the frequency distribution of velocity measurements across surveys to calculate the average percent availability of slow-water refuge habitat (early season habitat; flow <0.18 m/s), which previous studies have shown is an important predictor of salmon first-summer survival in this system (Nislow et al., 1999, 2000, 2004). We also measured stream gradient over each site with hand level and staff.

We sampled the full fish community at each site in July or August, either over the entire 100-m site (2003 and 2004) or a 40-m reach within the site (1997 and 1998). Fish sampling consisted of three or four pass removal electrofishing surveys with a Smith–Root BP-12 or similar electroshocker. During fish sampling, block nets at the ends of the sample reach prevented movement of fish in and out of the site. All captured salmonids and a subset of other species were weighed and measured, then held in in-stream livewells until sampling was complete, when they were returned to the stream. We used a maximum weighted likelihood method to estimate total abundance from removal sampling (Carle and Strub, 1978). Salmon and trout abundance was estimated separately for YOY and overyearling (1+) age classes (including both second and third-summer salmon), as separated based on stream-specific size distributions (usually YOY were <80 mm and 1+ were >100 mm). We did not count fish <30 mm total length (YOY dace and sculpin), as we did not capture them consistently. For three sites sampled in 1998, only salmonids were

enumerated. However, sculpin and dace densities were similar and highly correlated across years for all other sites (all $r > 0.84$, $n = 8$, $P < 0.01$), so we used the 1997 estimates for both years for these sites.

To evaluate predation on stocked salmon fry, we sampled sculpin and trout stomach contents at an additional seven sites (not used for population estimates) on the night salmon were stocked in 2004 and 2005. At each site, we started sampling 30 min after dusk and electrofished a 50 m reach, collecting only sculpin and trout. We captured few trout and removed their stomach contents by gastric lavage before returning them to the stream. Lavage was ineffective for sculpin, so sculpin were sacrificed and dissected to remove stomach contents.

2.3.   Data analysis

We treat each site-year as an independent observation in analysis as each year represents survival of an independent cohort stocked at the site, and sites were widely separated. Results are unchanged if we use site means across both years of sampling. We used end-of-summer YOY salmon density at each site as the primary response in analysis, log_{10}-transformed to linearize relationships and equalize variance. Final YOY density is a result of survival as well as movement of YOY salmon in and out of the sample reach. However, fry were scatter-stocked at even density throughout the entire stream and our sample reaches were representative of local habitat, so we assumed that net movement of salmon in and out of the sample reach over the summer was balanced. We did not adjust for different times between stocking and sampling as most salmon first-summer mortality occurs in the first few weeks after stocking (Nislow et al., 2004). Furthermore, stocking density (CV = 33%) varied little relative to final density (CV = 76%) and they were not correlated ($r = 0.13$, $n = 19$, $P = 0.60$), so most variation in density was driven by loss of salmon and not the number stocked. Thus, we treat YOY density as an index of salmon survival across sites.

We considered densities of the fish species common across most sites as potential predictors: brook trout, dace (sum of blacknose and longnose), and sculpin. Densities of brook trout YOY and 1+ were correlated ($r = 0.67$, $n = 19$, $P = 0.002$), so we used their combined density as a single predictor. We did not include the sole exotic species, rainbow trout, as it was only present at three sites (range of rainbow trout density 3–11 per 100 m^2). However, separate analysis of variance indicated that presence of rainbow trout was not associated with reduced YOY salmon survival ($F_{1,17} = 0.81$, $P = 0.38$). Mean stream width, depth, percent early season habitat, and gradient were initially considered as habitat predictors, but we dropped depth because it was highly correlated with width ($r = 0.75$, $n = 11$, $P = 0.008$). We used pairwise correlations to assess relationships between YOY density and all six predictors, with the P-value Bonferroni-corrected for multiple tests. To determine the independent contribution of each predictor after accounting for correlations among predictors, we used hierarchical partitioning of R^2 from all possible multiple regressions for all predictors (Mac Nally and Walsh, 2004; Walsh and Mac Nally, 2005); we assessed significance of hierarchical partitioning estimates

with a randomization test (10,000 independent randomizations of the predictors). We estimated the model-weighted average regression coefficient for each parameter across all models with weights >0.05 using Bayesian model averaging (Raftery et al., 2006). All statistical analysis was performed using R (R Development Core Team, 2006).

3. Results

Final density of YOY salmon ranged from 1–25 per 100 m^2 across sites; equivalent to first-summer survival rates of 2–78%. Sculpin density and early season habitat availability were the only predictors correlated with salmon first-summer survival in pairwise tests (Table 1). Salmon survival was higher in streams with few sculpin and more early season habitat (Fig. 1). Sculpin density and early season habitat availability were correlated to each other ($r = -0.48$, $n = 19$, $P = 0.04$). However, hierarchical partitioning showed that both sculpin density and early season habitat explained significant variation in salmon survival independent of other predictors (Table 1). Furthermore, multi-model inference confirms the strong negative relationship between sculpin and salmon survival. Model-weighted regression coefficients suggest that increasing sculpin density by ca. 50 per 100 m^2 reduces final salmon density by 50% (Table 2). In contrast to the correlation and hierarchical partitioning analyses, model-averaged coefficients indicate that brook trout density is positively related to salmon density, while habitat is a less important predictor (Table 2).

Across all seven sites where we sampled predator stomachs, 10% (9 of 91) of the sculpin stomachs contained salmon fry. Most sculpin that had consumed salmon contained multiple fry (mean: 2.8 fry, range: 1–4). Sculpin that contained fry ranged from 57–77 mm TL (salmon fry are ca. 20–25 mm TL when stocked). Densities of sculpin >57 mm TL ranged from 13–34 per 100 m^2 at the sites we sampled (Ward, unpublished data). Thus, we estimate losses to sculpin predation at these sites of 4–10 fry per 100 m^2, or ca. 8–20% of stocked fry, within the first few hours after stocking. We collected few trout in night-time sampling. Of eleven brook trout captured, three contained salmon fry (size range of predators: 97–110 mm TL; range of 1–8 fry per stomach).

Table 2 – Model-weighted average regression coefficients for all predictors of salmon survival (as log$_{10}$ final density) and the posterior probability that the coefficient does not equal zero

	Coefficient ± SE	Probability
Sculpin density	−0.006 ± 0.002	96
Brook trout density	0.03 ± 0.02	84
Dace density	0.001 ± 0.001	32
Width	0.01 ± 0.03	47
Gradient	0.01 ± 0.06	25
Early season habitat	0.76 ± 1.1	21

We used linear regression to determine whether sites with low first-summer salmon survival yielded fewer 1+ salmon recruits. Across all sites, higher survival in the first year of sampling led to higher 1+ density the next year (1+ per 100 m^2 = 0.51 + 0.35 YOY per 100 m^2, $r^2 = 0.57$, $n = 10$, $P = 0.01$), excluding one site where 1+ density was three times higher than YOY density the previous year, indicating unusually high immigration. At the low stocking density and survival rates we observed, compensatory mortality did not alleviate the effects of sculpin on salmon recruitment past the first summer.

4. Discussion

We found that a native generalist predator, slimy sculpin, was associated with significantly reduced survival of Atlantic salmon reintroduced into their historic rearing habitat. These results are consistent with other studies showing that predators and competitors can reduce the success of reintroductions of extirpated populations (e.g. Sinclair et al., 1998). However, while previous studies have clearly documented dramatic effects of some exotic species on reintroduction success, the effect of native species on rare and reintroduced populations gets relatively little attention in conservation studies (Garrott et al., 1993). The effect of native sculpin on salmon survival indicates that, even in the absence of exotic species, local community structure plays a key role in determining the success of reintroductions and recovery efforts.
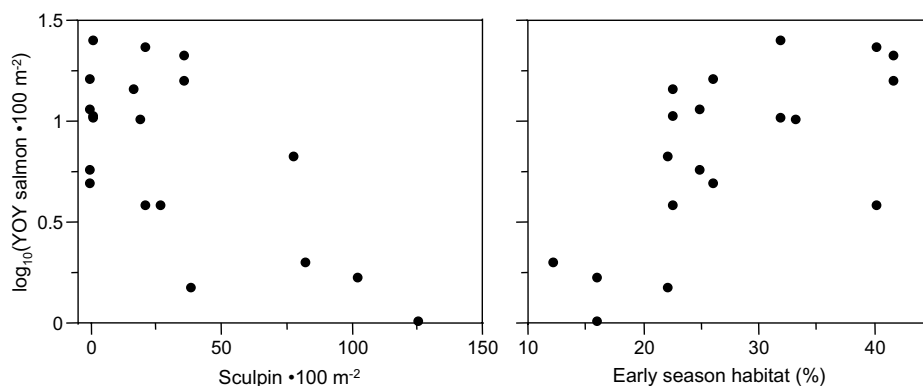

Fig. 1 – Density of young-of-the-year (YOY) salmon survivors related to (left) sculpin density and (right) the percent of stream area that is suitable slow-water refuge habitat during the early season. Each point in the scatterplot is one site-year.

4.1. Effects of sculpin on salmon

Sculpins in general were historically vilified as predators (e.g. Clary, 1972) and competitors (e.g. Brocksen et al., 1968) of salmonids, until Moyle (1977) reported that there was no evidence at the time that sculpins actually had any effect on salmonid populations. More recently, some studies have suggested that various sculpin species are associated with reduced recruitment of juvenile salmonids in other systems in North America and Europe (Olsen and Vollestad, 2001; Pender and Kwak, 2002; Elliott, 2006). However, no comparable previous work has addressed the interaction between slimy sculpin and Atlantic salmon (see Pihlaja et al., 1998; Gabler and Amundsen, 1999; Gabler et al., 2001 for other sculpin species). The effects of sculpins on salmonids are probably most severe for population reintroductions or for populations already suppressed by other factors, as sculpins regularly coexist with healthy salmonid populations (Moyle, 1977).

Slimy sculpin preyed on salmon fry, likely accounting for the impact of sculpin on salmon survival. Competition between sculpins and salmonids has also received some recent attention (e.g. Olsen and Vollestad, 2005), although recent small-scale experiments suggest competition with slimy sculpin has little effect on YOY salmonids (Ruetz et al., 2003; Zimmerman and Vondracek, 2006). In other systems, there is still some controversy regarding the extent to which sculpins prey on salmonid eggs and fry. However, it is increasingly clear that many sculpin species are effective predators of salmonids (Gaudin, 1985; Berejikian, 1995; Foote and Brown, 1998; Gaudin and Caillere, 2000; Mirza and Chivers, 2002; Tabor et al., 2004). We documented relatively low predation rates, but given the very high local density that sculpins can achieve and the low density of reintroduced fry in the study streams, even low predation rates have large impacts on salmon survival. In general, sculpin and other small-bodied fish are not considered important piscivores. Nonetheless, as abundant, opportunistic predators, even small fish can severely suppress survival of rare species by consuming vulnerable juveniles (Bestgen et al., 2006).

The effect of a species on reintroduction success is not easily predictable from knowledge of their interactions in other systems. For example, many previous studies show that brook trout compete with (Dickson and MacCrimmon, 1982; MacCrimmon and Dickson, 1983; Rodriguez, 1995) and prey upon (Mohler et al., 2002; Henderson and Letcher, 2003) juvenile Atlantic salmon. However, we, along with Raffenberg and Parrish (2003), found that, if anything, increased trout density is associated with increased survival of reintroduced Atlantic salmon. Brook trout may be a useful predictor of salmon survival because trout density integrates information about habitat characteristics such that trout are an indicator of suitable salmon habitat. Consistent with this hypothesis, our hierarchical partitioning analysis showed that brook trout density did not explain significant variation in salmon survival independent of habitat.

Given the important role of habitat modification in population extirpations, much of the effort in reintroduction programs is devoted to meeting habitat requirements for reintroduced populations. In the Connecticut River basin, constructing facilities for migrating salmon to pass dams and access spawning habitat was an essential first step towards population restoration (Gephard and McMenemy, 2004). For juvenile salmon, our results reinforce the important role of suitable early season habitat for fry as a key determinant of juvenile survival for reintroduced Atlantic salmon in the study system (Nislow et al., 1999, 2000, 2004). We cannot evaluate the extent to which key habitat characteristics in rearing tributaries have changed since salmon went extinct in the Connecticut River. However, such habitat alterations may directly affect salmon survival as well as exacerbate the effect of interactions with other species like sculpin. Other studies indicate that dams (Blackwell and Juanes, 1998; Petersen, 2001) and even anthropogenic streamside lighting (Tabor et al., 2004) can increase native piscivore impacts on salmon.

4.2. Conservation implications

Abundant, opportunistic, generalist predators like sculpin are particularly likely to interfere with reintroduction of extirpated species. Generalist predators that maintain high abundance when populations of endangered prey decline due to other causes often have severe impacts on the rare prey (Sinclair et al., 1998). Furthermore, captive-bred reintroduced populations that lack experience or adaptation with predators are particularly vulnerable (Berejikian, 1995; Griffin et al., 2000). The strong impacts of exotic generalist predators on reintroduced prey clearly illustrate that predators can reduce the success of reintroductions (Sinclair et al., 1998). Similarly, in other applied contexts native generalist predators contribute to the biotic resistance of native communities to exotic introductions (Levine et al., 2004; Gruner, 2005) and native generalist predators can prevent the establishment of organisms introduced for biological control (Goeden and Louda, 1976; Hunt-Joshi et al., 2005; Ward and Newman, 2006). Across all of these contexts, generalist predators are consistently a key determinant of introduction success.

Reintroduction programs can militate against effects of native predators by either reducing prey exposure to predators or reducing prey vulnerability to predators. Predator population control programs or smaller-scale predator exclosures can reduce exposure to predators, approaches typically applied to exotic predators (Moseby and Read, 2006; Knapp et al., 2007). However, controlling predator abundance is expensive, often fails, and may not be feasible or even desirable for native predators (Goodrich and Buskirk, 1995). In our study system, sculpins are entirely absent from some suitable salmon streams; for such patchily-distributed predators, concentrating introductions at such low predator-density sites can effectively reduce exposure to predators. Reintroduction programs can reduce vulnerability of reintroduced prey to predators by enhancing predator-avoidance behavior, either by avoiding captive breeding or training individuals prior to release (e.g. Mathews et al., 2005). Furthermore, low-density populations are particularly susceptible to generalist predators (Sinclair et al., 1998), so increasing release density to swamp predators at local scales may reduce losses of reintroduced populations to predation.

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