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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 populations 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

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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,

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

	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

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.