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Indirect effects of bioinvasions in Yellowstone Lake: The response of river otters to declines in native cutthroat trout

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ABSTRACT

Nonnative species threaten ecosystems throughout the world — including protected reserves. In Yellowstone National Park, river otters *Lontra canadensis* depend on native cutthroat trout as prey. However, nonnative lake trout and whirling disease have significantly reduced the abundance of these native fish in the park's largest body of water, Yellowstone Lake. We studied the demographic and behavioral responses of otters to declining cutthroat trout on Yellowstone Lake and its tributaries. From 2002-2008, we monitored otter activity at latrine (scent-marking) sites, collected scat for prey identification, and used individual genotypes from scat and hair samples to evaluate survival and abundance with capture–recapture methods. Otter activity at latrines decreased with declines in cutthroat trout, and the prevalence of these fish in otter scat declined from 73% to 53%. Cutthroat trout numbers were the best predictor of temporal variation in apparent survival, and mean annual survival for otters was low (0.72). The density of otters in our study area (1 otter per 13.4 km of shoreline) was also low, and evidence of a recent genetic bottleneck suggests that otter abundance might have declined prior to our study. River otters in and around Yellowstone Lake appear to be responding to reductions in cutthroat trout via changes in distribution, diet, and possibly survival and abundance. Our results provide a baseline estimate for monitoring the broader outcome of management efforts to conserve native cutthroat trout and emphasize the indirect ecosystem consequences of invasive species.

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1. Introduction

Nonnative species are a leading threat to biodiversity (Wilcove et al., 1998). Successful invaders may assume the role of "strongly interacting species" (Soulé et al., 2005) by directly affecting endemics, or via indirect effects on nutrient dynamics and ecosystem function (Mack et al., 2000). Furthermore, the effects of invaders in one ecosystem can be linked to ecological processes in an adjacent one (Knight et al., 2005). The establishment of formal reserves, such as national parks, may help attenuate the spread of nonnative species, but bioinvasions are a significant concern even in these relatively pristine settings (Loope, 2004).

Yellowstone National Park (YNP) has been one of the most protected natural areas in North America for over a century. Nonetheless, human-mediated invasions of nonnative species (e.g., Hall et al., 2006) have threatened habitats throughout the Greater Yellowstone Ecosystem (GYE). Recently, nonnative species created a potential ecological catastrophe in the park's largest body of water, Yellowstone Lake. Here, two aquatic invaders, lake trout (*Salvelinus namaycush*) and whirling disease (caused by the parasite *Myxobolus cerebralis*), led to a severe decline in the population of native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*; Koel et al., 2005). Cutthroat trout were historically a dominant species in this ecosystem and prey for numerous birds and mammals (Gresswell, 2011). The decline in cutthroat trout has altered the lake's trophic structure and likely had propagating effects throughout the Yellowstone Lake food web (Gresswell, 2011; Middleton et al., 2013). However, few studies have quantified the effects of these invaders on top predators.

The GYE has historically been a refuge for North American river otters (*Lontra canadensis*) when habitat loss, water pollution, and over-harvest reduced their populations in other parts of the Rocky Mountain region (Boyle, 2006). Otters are one of several species in Yellowstone Lake that depend heavily on native cutthroat trout for prey, especially during summer when the fish migrate from the lake into tributary streams to spawn (Crait and Ben-David, 2006; Wengeler et al., 2010). Since the introduction of lake trout, the Yellowstone Lake cutthroat trout population has declined by more than 90% (Koel et al., 2005; Teisberg et al., 2014). The lake supports relatively few fish species, and other potential prey are unlikely to provide a suitable replacement either because they are less abundant or because they have a lower energy value than trout (Crait and Ben-David, 2006). Moreover, introduced lake trout are less accessible to river otters because they inhabit deeper water and spawn in the lake rather than in streams (Koel et al., 2005). Continued declines in the availability

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of cutthroat trout could therefore reduce the abundance and distribution of otters around Yellowstone Lake.

To explore the effects of changes to the Yellowstone Lake food web on river otters, we monitored seasonal activity at latrine (scent-marking) sites, evaluated diet composition, and estimated survival and abundance via noninvasive genetic sampling of feces and hair. We predicted that (1) declines in the cutthroat trout population would reduce abundance and survival of river otters in the Yellowstone Lake watershed; (2) river otter activity levels would be lowest in areas of the lake ecosystem with the fewest cutthroat trout; and (3) concurrent with cutthroat trout declines, the frequency of other prey items in otter scats would increase during the study.

2. Methods

2.1. Study area

Detailed descriptions of the study area are available in Crait and Ben-David (2006, 2007). Briefly, Yellowstone Lake is located in southeastern YNP, Wyoming, USA (Fig. 1). YNP has a temperate climate with a mean annual temperature of 0 °C. Summer and winter temperatures average 11.1 °C and −10.8 °C, respectively. Mean annual precipitation is 513 mm — primarily falling as snow in late fall and winter (Benson, 1961). Yellowstone Lake is a large (surface area = 341 km^2; shoreline length = 239 km) and deep (average 48.5 m; maximum 133 m), mesotrophic lake, located at high elevation (2357 m).

Yellowstone Lake supports two native fish species: Yellowstone cutthroat trout and longnose dace (*Rhinichthys cataractae*), as well as nonnative longnose sucker (*Catostomus catostomus*), redside shiner (*Richardsonius balteatus*), lake chub (*Couesius plumbeus*), and more recently, lake trout (Koel et al., 2005). In late spring and early summer, adult cutthroat trout migrate into ~68 of the 124 of the lake's tributaries to spawn. Spawning adults remain in streams from 1–3 weeks, and most migrate back to the lake after spawning (Gresswell, 2011).

Nonnative lake trout were first discovered in Yellowstone Lake in 1994, and have been breeding there since the mid to late 1980s (Koel et al., 2005). Individual lake trout consume an average 41 cutthroat trout per year (Ruzycki et al., 2003) and contributed to ~60% declines

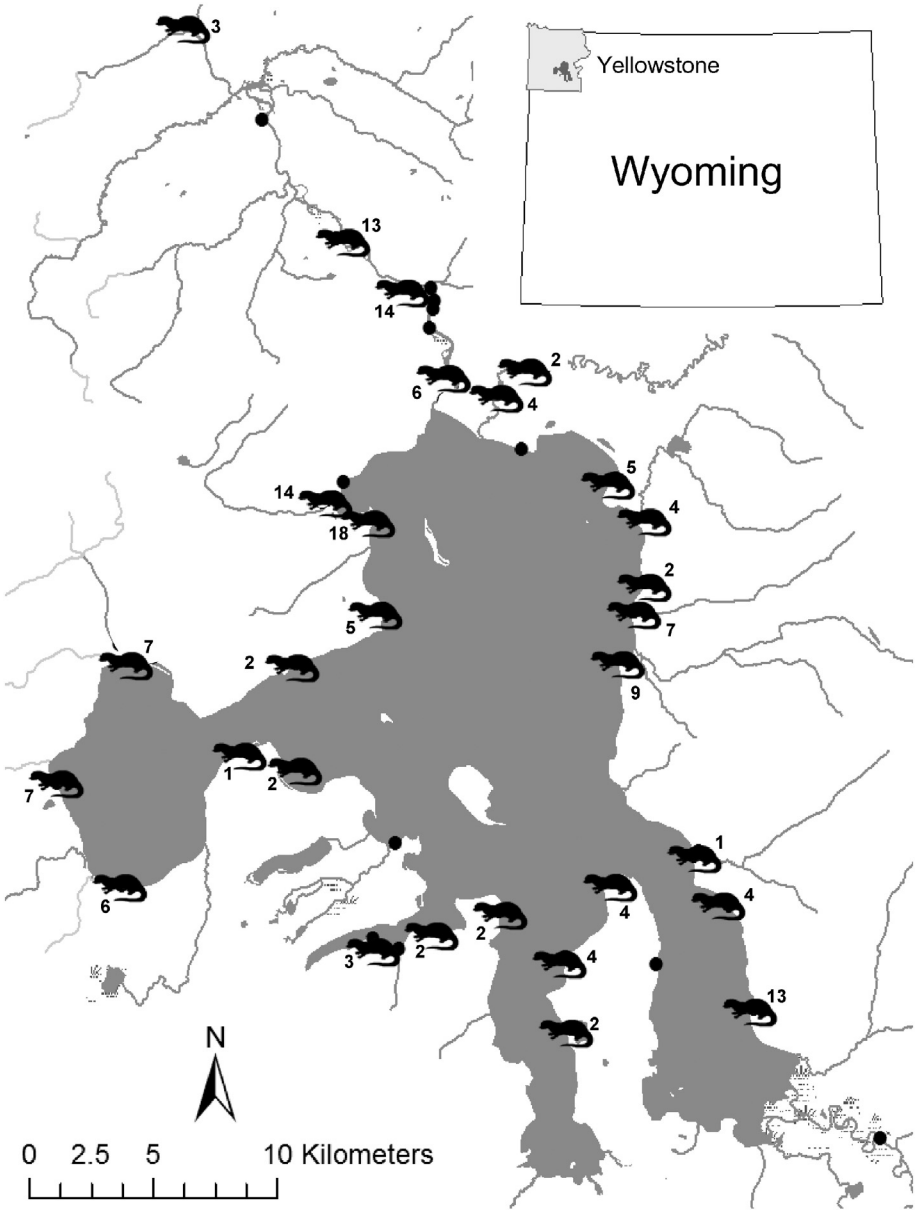

Fig. 1. Location of study area and river otter latrine sites around Yellowstone Lake, in Yellowstone National Park, Wyoming, USA in summer 2002–2010. Otter symbols denote number of individuals identified on latrines. Dots represent active latrines from which individual genotypes were not obtained (following Haroldson et al., 2005).

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