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Evidence of indirect impacts of introduced trout on native amphibians via facilitation of a shared predator

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ABSTRACT

Hyperpredation occurs when non-native prey facilitate invasive predators, which then suppress native prey. Direct impacts of introduced fish on amphibians are well studied, but the role of fish in supporting shared predators has not been considered. We present evidence for indirect effects of trout on amphibians through snake predation. Analyses of the diet, distribution and density of the Pacific coast aquatic garter snake (*Thamnophis atratus*) relative to the sympatric common garter snake (*Thamnophis sirtalis*) in the Klamath Mountains of California suggest that trout introductions facilitated expansion of *T. atratus* by providing alternative prey. *T. atratus* diet included trout and amphibians whereas *T. sirtalis* preyed solely upon amphibians. The distribution and density of *T. atratus* matched that of introduced trout instead of native amphibians. Populations of *T. atratus* could reach high densities in the absence of high densities of amphibians. When the snakes opportunistically prey upon amphibians whose numbers are already directly impacted by trout, they can cause significant additional declines. When *T. atratus* was present in lake basins, native Cascades frogs (*Rana cascadae*) were rarer than in basins without *T. atratus*. This case differs from other hyperpredation studies because the two prey species also interact via intraguild predation. Given the worldwide practice of stocking fish into aquatic habitats, it is important to understand the consequences of the practice on food-web structure and ecosystem functioning. Bottom-up impacts of introduced predators should be considered as well as top-down so that managers can incorporate the range of ecosystem-level effects into conservation goals and decisions.

1. Introduction

A predator's impact on prey abundance can range from inconsequential (e.g., Cardona, 2006) to severe (e.g., Halpern et al., 2006). Strong top-down effects often occur when alternate prey sources support increased densities of generalist predators, which then depress local prey populations (Polis et al., 1997; Sinclair et al., 1998). When the renewal rate of alternate prey is high then predators are assured a food supply they cannot overexploit. As a consequence, predator success becomes decoupled from local consumer-resource dynamics (Schoener and Spiller, 1996; Polis et al., 1997). This form of apparent competition (Holt, 1977) or indirect amensalism (Chaneton and Bonsall, 2000) is known for several systems.

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For example, deep-sea fishes periodically migrate into shallow waters where they provide an alternate prey for sea otters, which then depress local sea urchin populations (Watt et al., 2000). Apparent competition can also be induced by humans in the form of introduced species. For example, the introduction of feral pigs to the California Channel Islands has sustained an unnaturally large population of predatory golden eagles. Golden eagles also prey upon the endemic island fox, reducing its numbers to near extinction (Roemer et al., 2002).

The ecological importance of facilitation of predators by non-indigenous prey and the resulting indirect effects have only recently been highlighted (Noonburg and Byers, 2005; Rodriguez, 2006). "Hyperpredation" refers to the indirect interactions between non-indigenous and native prey via a shared predator (Smith and Quin, 1996; Courchamp et al., 1999) and occurs when a non-indigenous prey species indirectly facilitates the decline of a native prey species by enabling a shared predator to increase in abundance (Smith and Quin, 1996). The shared predator often moves into the habitat of the indigenous prey by following the expansion of the non-indigenous prey (Courchamp et al., 2000).

Most studies on introduced predatory species focus on their direct effects on native biota. For example, the direct negative effects of introduced fish on native amphibian distribution and abundance in mountain lakes have been studied extensively (e.g., Vredenburg, 2004; Welsh et al., 2006; Knapp et al., 2007). Additional studies have found top-down cascading indirect effects due to fish introductions (Scavia et al., 1986; Knapp et al., 2001; Schindler et al., 2001). All of these studies consider trout only as predators.

We take an alternate approach and focus on introduced trout as a supplemental prey source that facilitates the increase and spread of the Pacific coast aquatic garter snake (*Thamnophis atratus*), a species that preys on both fishes and amphibians (Lind and Welsh, 1994). The introduction of a common, supplemented (via stocking) prey source in mountain lakes of northern California may have allowed *T. atratus* to expand its range upslope from its more typical lower elevation stream habitats (Rossman et al., 1996; Fitch, 1984) into these historically fishless lentic habitats. In this region, steep canyon gradients created during Pleistocene glaciations prevented colonization by fishes into lakes higher than 1500 m in elevation (Welsh et al., 2006). Beginning in the 1800 s, various salmonids (primarily *Oncorhynchus*, *Salmo*, and *Salvelinus* spp., hereafter "trout") were introduced to lakes for recreation and stocking continues today. We hypothesize that there are indirect consequences of introduced trout in the high elevations of the Klamath Mountains of northern California by means of increased predation on the Cascades frog (*Rana cascadae*) by *T. atratus*. *R. cascadae* is a native lentic breeding amphibian in high elevations of the Klamath Mountains and is a known prey item of introduced trout (Simons, 1998) and garter snakes (Garwood and Welsh, 2005).

This study expands on previous studies of hyperpredation (Smith and Quin, 1996; Courchamp et al., 2000; Roemer et al., 2002; Kristan and Boarman, 2003) by including two prey species that also interact via intraguild predation (when species pairs have both competitive and predator/prey interactions; Polis et al., 1989). *R. cascadae* may be especially sensitive to hyperpredation by *T. atratus* because it already has depressed population numbers due to trout (Welsh et al., 2006). In addition, the frog requires at least semi-permanent water throughout its life, making all life stages vulnerable to aquatic garter snake predation.

We evaluate the hyperpredation hypothesis by comparing the diet, distribution, and density of the facilitated predator (*T. atratus*) with another native garter snake species, the common garter snake (*Thamnophis sirtalis*). Although *T. sirtalis* occurs in a wide range of habitats and has a broad prey base range-wide, it has been found to be a local amphibian specialist in high elevation lentic habitats (Kephart, 1982). Based on existing literature, we predicted that the diet of *T. sirtalis* in the Klamath Mountains would consist primarily of amphibians (Kephart, 1982; Rossman et al., 1996), while the diet of *T. atratus* would consist of both introduced trout and amphibians (Lind and Welsh, 1994). By eating trout as well as native prey, *T. atratus* populations would be able to succeed regardless of native prey densities. In contrast to *T. sirtalis*, the distribution and densities of *T. atratus*, therefore, should not be strongly related to densities of native prey. Where *R. cascadae* co-occur with trout, the additional predation pressure by *T. atratus* could be detrimental to *R. cascadae* populations. We assess the potential impacts to *R. cascadae* by comparing the relative density of frogs in trout-containing basins with and without additional predation by *T. atratus*.

2. Materials and methods

We make use of three datasets collected from the Klamath Mountains between 1999 and 2006: the first is a large-scale snapshot census of lentic habitats throughout three wilderness areas (landscape survey), the second involves repeated sampling of 16 Trinity Alps Wilderness headwater basins over four years (basin study), and the third is a detailed case study in one sub-watershed consisting of a lake, several permanent ponds, and a complex wet meadow system systematically sampled for four years (case study, Fig. 1). The combination of datasets allows us to compare patterns across spatial scales and with different levels of detail.

2.1. *Landscape survey*

The main goal of the landscape survey was to document distributions and relative abundances of introduced trout, amphibians and garter snakes throughout the lentic water bodies (lakes, ponds, and wet meadows) of the Trinity Alps, Marble Mountains, and Russian wilderness areas (Welsh et al., 2006). All three of these wilderness areas are within the range and habitat of *R. cascadae*. Until recently, approximately 90% of lakes greater than 1 ha in these wildernesses were stocked with trout on an annual or biennial basis. Since 2002, the California Department of Fish and Game (CDFG) suspended stocking in approximately half of the lakes to assess the impacts and sustainability of introduced trout.

During the summers of 1999–2002, we surveyed 728 water bodies between 1525 and 2290 m in elevation, mostly within sub-alpine habitats. Because of the high number of water bodies and their remoteness, each site was sampled only once. The presence or absence and estimated density of trout