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Assessing the long-term causal effect of trout invasion on a native charr

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ABSTRACT

Many studies have indicated that invasive species can drive declines in native species through interspecific competition. In freshwater ecosystems, brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) have been implicated in reducing native species, especially congeneric salmonid fishes. However, demonstrating causality in the wild is problematic because non-natives might replace natives in areas where the former were extirpated by other environmental changes. Using the recently developed technique of multispatial convergent cross mapping (CCM) and a long-term monitoring data set (2002–2017) with spatial replication on both introduced and native salmonids in a Japanese stream, I tested whether an increase in non-native trout caused a decrease in native charr (*Salvelinus leucomaenis*). Native charr decreased their population density over time in contrast to the non-native brown trout and rainbow trout. The dominant species changed from native charr (64%) in 2002 to non-native trout (97%) by 2017. Multispatial CCM identified significant causal forcing of the native charr by both rainbow trout and brown trout, lending support for the hypothesis of displacement, rather than replacement, of a native species by non-native species. These results therefore suggest that eradicating the invasive trout species may aid the recovery of native charr in the region.

1. Introduction

Understanding the long-term effects of species invasions on native biota is important because the emerging impact of a particular invasion may not be recognized immediately and often changes over time (Strayer et al., 2006). Even though the impacts of non-native species may become a matter of public knowledge, most previous studies on species invasion have lacked a temporal context (Strayer et al., 2006). Expansion of invasive species can drive declines in native species through predation, the introduction of pathogens, and inter-specific competition (Davis, 2003; Bøhn et al., 2008; Dias et al., 2017); however, demonstrating the causality of species replacement is not easy. Non-natives can play an active role in the extirpation of natives (i.e., displacement), yet non-natives may also colonize areas where natives have been extirpated by other factors, such as climate change or anthropogenic impact (i.e., replacement) (Dunham et al., 2002).

Some fishes are extensively introduced into non-native regions for the purposes of enhancing food resources or sport fishing, which in turn leads to homogenization of the fish fauna across geographically separate regions, thereby posing a threat to biodiversity (Rahel, 2000). Brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), which originate from Europe and North America, respectively, have become established on five continents and several large islands, and they are included on a list of ‘100 of the world’s worst invasive alien species’ by the IUCN (Lowe et al., 2000). While these cosmopolitan species offer a variety of social and economic benefits to humans, both brown trout and rainbow trout have been implicated in reducing native species, especially congeneric salmonids (Fausch, 1988; Fuller et al., 1999; Kitano, 2004; Baxter et al., 2007). Although many studies indicated that displacement was the mechanism, the alternative hypothesis of replacement has rarely been tested in the field (Dunham et al., 2002). For example, global warming could be a major concern for the decline of native charrs (*Salvelinus* spp.), whereby during summer the upper thermal limits maybe exceeded for this species, which has an optimal temperature range that is lower than those for most other salmonids (Nakano et al., 1996; Isaak et al., 2010).

Convergent cross mapping (CCM) is a recently developed technique to identify causal relationships in nonlinear systems, such as instances of interspecific competition (Sugihara et al., 2012). Though CCM typically requires time series with at least 30 sequential observations, the multispatial CCM technique adapted by Clark et al. (2015) using the method of Hsieh et al. (2007) is an expansive method capable of analyzing relatively short time-series data to leverage spatial replication. Here, I applied the recently developed technique of multispatial CCM to test whether an increase in non-native trout caused a decrease in native charr. Using multispatial CCM and a data set from long-term monitoring (2002–2017) of both the introduced and native salmonids in a Japanese stream, I show that non-native rainbow trout and brown trout displaced a native salmonid (*Salvelinus leucomaenis*).

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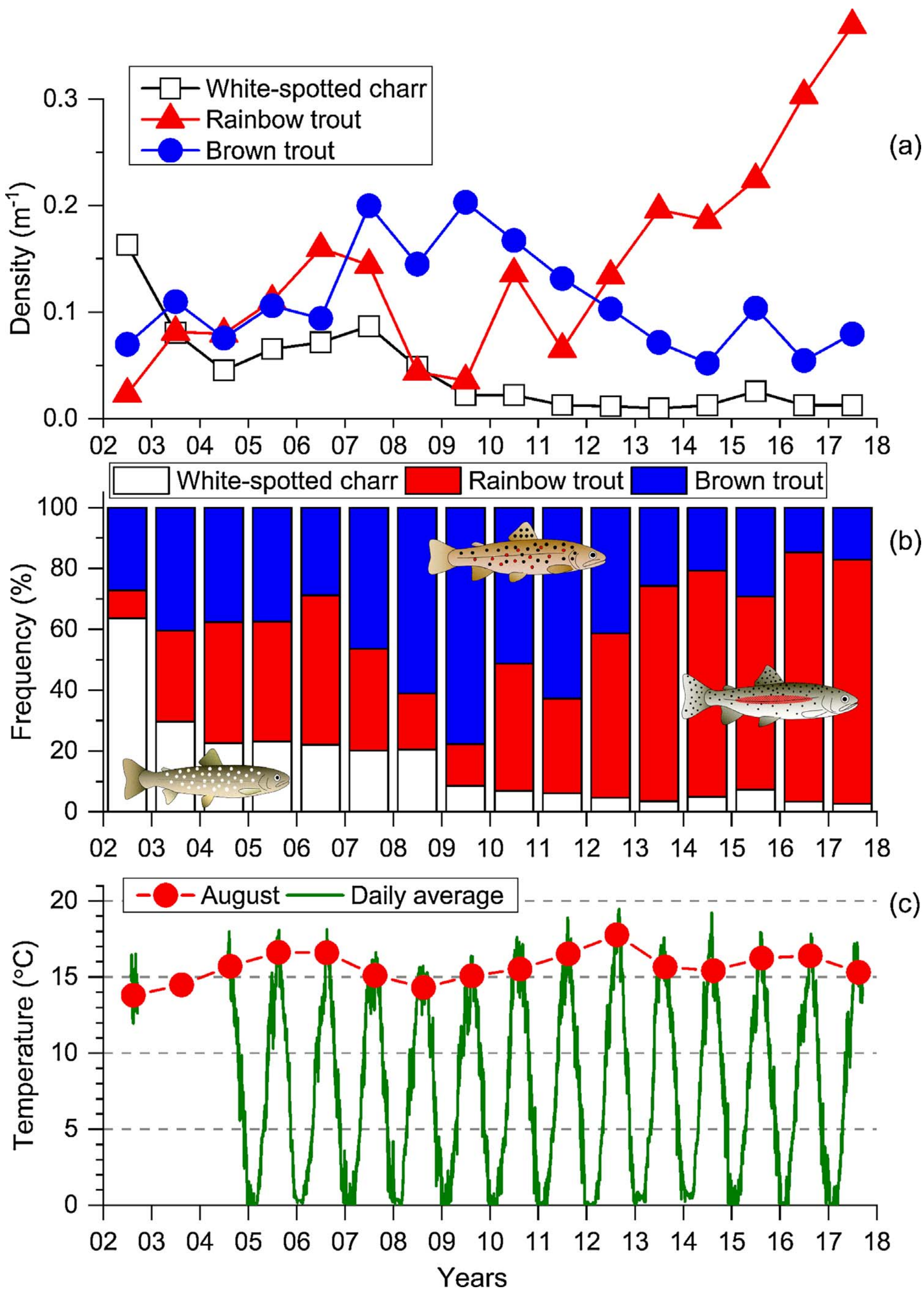

Fig. 1. Decadal changes in the fish assemblage and water temperature in the Hekirichi River, Japan. (a) Population densities of native white-spotted charr, non-native brown trout, and non-native rainbow trout. (b) Relative frequencies of the three salmonids. (c) Daily and average August temperatures.

2. Methods

The study was conducted in the headwaters of the Hekirichi River, Hokkaido, Japan (N41°53′–41°54′, E140°31′–140°35′) (see map in Morita et al., 2004). Brown trout had been introduced into the system in 1989–1991, and rainbow trout were introduced in 1994–1998 (Tsuboi and Morita, 2004). Initially, white-spotted charr was the only native salmonid in the river reaches studied. A preliminary survey showed that the native white-spotted charr constituted 83% of the fish assemblage in 2001 (Tsuboi and Morita, 2004).

I established 30 study reaches (44 ± 15 m, mean ± SD), with each consisting of one pool and one riffle, except for two reaches with only pools. The combined length of the study reaches was 1.3 km. I conducted fish counts in the study reaches by underwater observations with snorkeling gear, during the summers from 2002 to 2017. During the daytime and equipped with a wetsuit, mask and snorkel, I entered the stream at the lower end of each reach and crawled slowly upstream in a zigzag pattern. The numbers of fish encountered were tabulated by species, except for the newly emerged salmonid fry (age 0+ years, < 70 mm in length). The same protocol was followed since 2002 (Morita et al., 2004). A total of 6 039 fish were observed. Fish density was measured for each species as the total number of fish observed per stream length. Of the 30 study reaches, 27 reaches were censused for all years; the time-series density data on the 27 reaches were used for the multispatial CCM analysis.

Water temperatures were measured in 2002 in summer only, and throughout 2004–2017 at hourly intervals at the most upstream reach, using data loggers (Stow-Away TidbiT, Onset Computer Corp., USA). The summer water temperatures in 2003 were estimated from the air temperature and precipitation measurements at a nearby weather station (Hokuto City): $Tw = 0.486*Ta - 0.691*10^{-2}*Q + 6.131$ ($R^2 = 0.665$, $P < 0.01$, $n = 15$), where Tw and Ta were water