

Effects of a range-shifting caddisfly on life histories of a top predator in high elevation ponds

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Abstract

Climate change is creating the opportunity for various species to undertake range expansion, both geographically and elevationally. There has been relatively little research into the ecological effects of these climate-driven range expansions on predators, particularly when the new species to a community fills a phenological gap in prey. The opportunity to learn more about these effects comes in a recent range expansion of a caddisfly species, *Nemotaulius hostilis*, into a well-studied, high elevation pond complex. I explored how this new species might be influencing the growth and life history of a top keystone predator, paedomorphic tiger salamanders. Using mark and recapture and comparing current collected data to that collected before *N. hostilis* was abundant, I tested how abundance of a new prey source is affecting salamander ecology. By understanding how a range extension influences top predators, we can gain insight into the direct and indirect effects of climate change on aquatic ecosystems.

Introduction

Climate change and the associated warming temperatures are beginning to cause significant changes in ecosystems around the world (Vitousek 1994, Ojima et al 1991). Species are moving into areas that were previously inhospitable to them, whether due to temperature, precipitation, or other environmental factors (Freeman et al 2018). There are several documented instances of species, both plant and animal, moving up in latitude or elevation to enter new habitat or to follow climate demands (Chen et al 2011, Freeman et al 2018). While some of these species may have similar life histories and niches to existing members of the affected communities, there are also range-expanding species that don't match up phenologically with the existing community in which they are moving (Gallinat et al 2021). Research is just beginning to explore the consequences of these range expansions on the ecosystems that they enter.

One example of such a range extension has occurred with *Nemotaulius hostilis*, a species of caddisfly native to Colorado. *N. hostilis* has a unique life history when compared to other local species, including those that have experienced range expansions previously. While most of the other caddisfly species overwinter as eggs, *N. hostilis* overwinters as larvae and grow more quickly than other overwintering species, filling a gap in the typical phenology of the ponds, and providing a potentially large, new food source for overwintering predatory tiger salamanders (*Ambystoma tigrinum nebulosum*) (Klemmer et al., unpubl. data). As of yet, there has been no research conducted on how filling this phenological gap may affect tiger salamander life histories.

Tiger salamanders have been studied at the Mexican Cut Nature Preserve, owned by the Nature Conservancy, since the 1950s, and have been individually marked since 1990 (Billick 2020, Wissinger and Whiteman 1992). They are long-lived and often slow-growing, with the oldest salamanders living into their thirties. They have two distinct morphs, a terrestrial metamorph and an aquatic paedomorph (Whiteman et al 2012). Because this project is focused on the effects of *N. hostilis*, particularly on their effects as larvae during the fall, winter, and spring, paedomorphs are the primary study morph, since they are the ones that overwinter in permanent ponds with *N. hostilis*.

Paedomorphs have been shown in preliminary research to predate *N. hostilis* into the fall (Whiteman et al. unpubl. data). As such, it is possible that these salamanders are feeding on the caddisfly larvae in the late fall, winter, and early spring, times when they previously would not have had an abundant prey source. This study focuses on determining whether there have been shifts in salamander body condition and population dynamics in the years since *N. hostilis* was first observed at Mexican Cut.

In this study, historical data on size and body condition was analyzed to determine if there is an upward trend in either of these factors of growth. The goal of this analysis was to determine if there was significant positive change in body condition, which could be an effect of the growing

N. hostilis population. Additionally, a foraging experiment was conducted to understand how predation rates vary between three common species of caddisfly in the Cut, including two species that are recent climate-driven invaders. Given the differences in case structure between each species, as well as differences in distribution across ponds with paedomorphic salamanders, we expected to see differences in salamander predation between the species.

Methods

The observational and experimental methods used at Mexican Cut have been established and consistently used since 1990 (Wissinger and Whiteman 1992, Whiteman et al. 2012, Lackey et al 2019).

Population Sampling

In order to obtain animals, salamanders were scooped out of a given pond using a long handled net and then brought back to a Weatherport for processing. To process, the salamanders were first checked for a passive integrated transponder (PIT) tag, which is a microchip with a unique number assigned to it, or for a unique toe clip (Brown et al 2022). These numbers or clips are linked to an individual salamander in the long-term database used by researchers at the Cut. If an animal does not have a PIT tag or clips, and is able to receive one at the time, they are given one once measurements are completed. The salamanders were weighed and measured for snout-vent length (SVL) and total length with a measuring board. We also recorded gill health (if applicable), body condition, morph, sex, and whether the salamander was reproducing (determined via cloaca condition). All measurements were recorded into an Access database, along with whether the salamander was a recapture or not. Once all of the salamanders from a pond were processed, they were taken back to the same pond and released.

Body Condition Analysis

The comprehensive database contains data on individual salamanders since 1990. In this study, the database was used to calculate body condition over time to determine how *N. hostilis* might be affecting the salamanders' health and populations. We focused on Ponds 1, 5, and 12 as these three have historically had the largest populations of paedomorphic salamanders. In order to control for both animals with no previous record and for multiple captures of the same animal in a year, the entire database was filtered by first capture and recaptures.

Body condition was calculated by dividing the mass by the snout-to-vent length (SVL) (Whiteman et al. 2012). An ANOVA with Satterthwaite's method was run using R to determine whether pond, salamander density, or some interaction of these three variables were significant factors in salamander body condition.

Commented [1]: But did we do this? Or was the analysis just on pond and density? It seems the latter, and if true then we should just focus on that. But the question really is how do things change pre- and post-invasion, so we will probably want to reanalyze with that in mind. You can certainly say what you see, but it won't mean much until we can analyze it.

I do not want you doing anymore analysis, I am just trying to make sure where we are with the science.

Foraging Experiment

Twenty-four plastic sweater boxes were set up at Mexican Cut; these boxes were filled with filtered water from Pond 8. The lids of each box were labeled using masking tape and each box was leveled using rocks. Caddisflies were captured by the bug crew with D-nets in two ponds (1 and 32). Two species of caddisfly were used in this experiment, *Limnephilus externus* and *L. picturatus*. Twelve of the twenty-four sweater boxes received ten *L. externus* each, while the other twelve boxes received ten *L. picturatus* each. Similarly, twelve paedomorphic salamanders were caught out of Pond 1. Salamanders were scanned for a PIT tag and measured; if a given salamander was between 78-83 mm, the salamander was weighed and set aside to be used in the experiment. There was no significant difference between salamander body sizes among treatments ($p > 0.05$). The twelve salamanders were randomly assigned to the sweater boxes, with six put into boxes containing *L. externus* and six put into boxes containing *L. picturatus*. The time at which the salamanders were placed into the boxes was recorded.

In total, the boxes were checked five times. Each time, all living caddisflies were counted, making note of missing and empty cases; this process was completed for all containers to account for any cannibalism within controls. After forty-eight hours, the caddisflies were counted for the last time, and the salamanders were removed and returned to Pond 1. The water from the boxes was filtered through a net to catch the remaining caddisflies, which were released to the pond they came from.

N. hostilis was not available for these experiments because of their unique phenology, but we plan to repeat this experimental design in September 2022. A two-way ANOVA was conducted on the data from the last count.

Results

Body Condition

There was a significant effect of individual ponds ($F = 3.67$, $p = 0.03$) and salamander density ($F = 5.16$, $p = 0.03$) on body condition growth but the interaction was not significant ($F = 1.28$, $p = 0.28$) (Fig. 1). Figure 1 was used to observe any trends up or down in body condition change over the course of past research done at Mexican Cut. There was a large amount of fluctuation in body condition growth observed by pond and from year to year, but the general trend is a decline in body condition until the last year, in which paedomorphic salamanders from two of the three permanent ponds showed sudden increases in their change in body condition, corresponding to the recent increase in *Nemotaulius* larval densities.

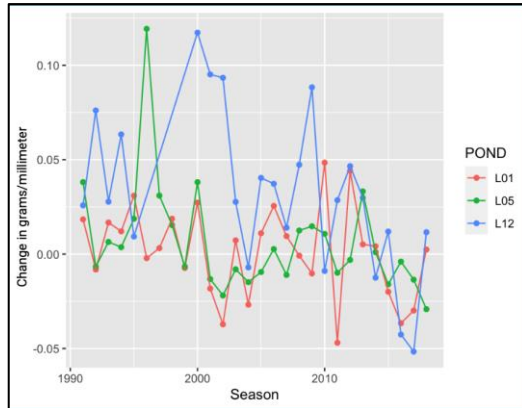


Figure 1. The average change in grams/millimeter by pond from 1990 to 2022.

Foraging Experiment

There was a significant interaction between caddisfly species and salamander presence ($F = 8.5$, $p = 0.009$). Over 48 hours, paedomorphic salamanders consumed significantly more *L. picturatus* (Fig. 2A) than *L. externus* (Fig. 2B), although both species were negatively affected by salamander predation..

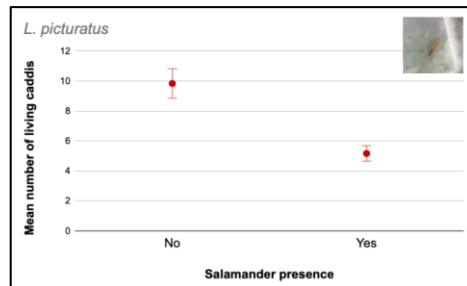


Figure 2A. Mean number of living *L. picturatus* after 48 hours as a function of salamander presence/absence.

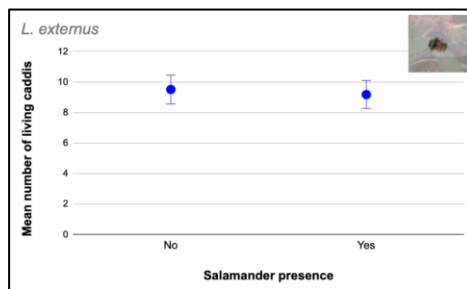


Figure 2B. Mean number of living *L. externus* after 48 hours as a function of salamander presence/absence.

Discussion

The ecosystem effects, particularly interactions between top predators and prey, of elevational range shifts has been increasingly observed in recent years, yet research has been slow to address the topic. By studying the effects of the recent caddisfly range expansion into the Mexican Cut, we began the process of understanding how a new food source could cause changes in salamander size and body condition.

There may be a bit of a delay in changes one might expect to see in predator populations following a prey increase (Bonsall and Hassell 2007). Put into context in this scenario, it is possible that the upward tick seen in the later parts of Figure 1 could be the front tail of a dramatic increase in change in body condition following observed increases in *N. hostilis* numbers in several of the permanent ponds over the last two years. As shown by Figure 1, there has been a general negative trend in body condition over the last 32 field seasons in all three

permanent ponds considered in this analysis. In the last 2-3 years, however, there has been an increase in body condition in two of the ponds (1 and 12). Assuming that *N. hostilis* is the variable affecting the salamander populations in a positive way, then a few more years worth of data could show a much stronger upward trend than the current research shows. Furthermore, body condition makes up just one measure of the effects of *N. hostilis* on salamander ecology in these ponds. Additional analysis on salamander abundance from year to year in different ponds, as well as survival rates by pond, would provide valuable insight into the potential effects of *N. hostilis* on the population as a whole. Lastly, it could prove insightful to have a closer look at the *N. hostilis* numbers and distributions over the years and into the future; the salamander populations might experience relatively low effects from *N. hostilis* while still affecting the caddisfly's populations significantly.

The foraging experiment was designed to evaluate whether salamanders varied in their foraging rates across different caddisfly species. Given the results of the analysis, Arizona tiger salamanders have much higher foraging rates on *L. picturatus* than *L. externus*. This variation is likely due to the differences in case construction between the species. *L. externus*, the species native to the Cut, creates large, 'fluffy' cases that can be much larger than a salamander can swallow or fit within their mouth. *L. picturatus*, on the other hand, has a narrow, thin case that allows salamanders to either suck them out of their case or swallow the entire case and larva. *L. picturatus* had also undergone a range expansion in years prior to the expansion by *N. hostilis*. It has been shown that species who undergo range expansions have differing responses to new predators, with some having more success at avoiding predation than others, so the differences in predation between *L. externus* and *L. picturatus* may be an example of an expanding species failing to adapt to or manage predation by the top predator of their new ecosystem (McPeck et al 1996, Zebbs et al 2022). Assuming that the observed preferences and a difference in response to new predators holds true for *N. hostilis*, then it is possible that the same experiment may show similar results. I hypothesize that a similar graph created for *N. hostilis* might look something like Figure 3.

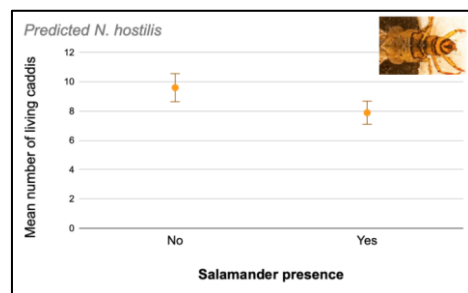


Figure 3. Mean number of living *N. hostilis* after 48 hours as a function of salamander presence/absence.

We plan to test this hypothesized graph by running another foraging experiment with *N. hostilis*, using the same methods outlined in the Methods section above, this fall. Given the time of the year, there may be some environmental factors, such as the ambient temperature's effects on salamander activity or a relative lack of other caddisfly species during the fall, that could affect the results of this test. Running the same experiment with *N. hostilis* in a similar instar to those used in this foraging experiment will be the next phase in determining salamander predation on the new caddisfly species.

This study is among the first to help us understand the community effects of the *N. hostilis* range expansion. However, the end result of continued study on this particular system could provide insight into how elevational range expansions affect mountain ecosystems worldwide. The extent of previous research and data that has been done at Mexican Cut is unique and provides enough information to compare the ecosystem before and after a new species arrived. Climate change and the subsequent temperature shifts will continue to create opportunities for range expansion, and it is only through continued research into the effects of previous expansions that the long term effects of those movements will be understood.

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