

Effect of abiotic microhabitat conditions on the coastal giant salamander *Dicamptodon tenebrosus* body size and density across and within streams

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ABSTRACT

Changes in the abiotic characteristics of a habitat can impact feeding behavior of top predators, triggering top-down trophic cascades. Coastal giant salamanders (*Dicamptodon tenebrosus*) are of particular interest due to their importance to California riparian habitats and their sensitivity to such abiotic changes. Our research studies the ways in which different creek systems and the presence of other *D. tenebrosus* larvae affect the growth and density of remaining larvae. We predicted that *D. tenebrosus* population density and body size would be highest in creek pools with the highest rock cover density and lowest in pools with the most silt. Furthermore, we predicted that larger creeks would have more cover rocks, which would correspond to higher densities and body sizes, while smaller creeks would have more silt, corresponding to lower densities and body sizes. We surveyed *D. tenebrosus* across three northern California (USA) streams with varying substrates and flow rates to examine the effect of abiotic factors on larval population density and body size. We found that larval density increased with rock density, that silt has little to no correlation to *D. tenebrosus* abundance, and smaller creeks significantly decrease the size of larvae. We also found that as salamander density increases, so does the size of salamander larvae and that the presence of a larger salamander increases the size of remaining salamanders. Conservation efforts of *D. tenebrosus* must thus incorporate maintenance of microhabitat conditions, such as substrate composition and water flow.

Keywords: creek substrate, *Dicamptodon tenebrosus*, body size, population density, top predator, amphibian ecology

INTRODUCTION

Changes in the population of top predators can have far-reaching effects on lower trophic levels via a trophic cascade (Baum and Worm 2009). These changes are caused by factors like relative body size or

abundance which affect top predator feeding behavior in a top-down ecosystem, in which consumers control behaviors and densities of species lower in the food web (Mäntylä et al. 2011). For example, density reductions of cod fish (*Gadus morhua*), a top predator, have led to larger populations of

smaller predators occupying lower trophic levels, such as herrings (*Clupea harengus*) and macroinvertebrates, by predator and prey release. Such density reductions in cod were caused by overfishing. Another study found that anthropogenic habitat destruction reduced predatory bird populations, which in turn triggered a trophic cascade that further released florivorous invertebrate populations, intensifying damage to plant populations (Mäntylä et al. 2011). Studies on trophic cascades often focus on changes in the population density of key species such as top predators in response to changes such as habitat destruction or alteration. Less understood are the effects of factors that impact predator function, such as size, which may in turn trigger trophic cascades.

An example of body size demographic changes affecting top-down control is seen in the common whitetail dragonfly (*Plathemis lydia*) (Rudolf 2012). Increased diversity of size classes in populations of the whitetail drove changes in top-down trophic control by promoting cannibalism of smaller individuals, which in turn promoted anti-predator behavior in these smaller individuals. In this way, the largest dragonflies controlled the behavior and abundance of the lower trophic level, consisting of the smallest whitetails. Furthermore, conspecific predation reduced predation pressure on other insect species, indicating larger trophic effects as a result of population-level changes in body size. Although in this example, whitetails underwent seasonal changes in body size demographics, it may be that habitat changes also affect predator body sizes, not just predator population density.

Effects of habitat changes on body size have been studied in organisms of intermediate trophic levels, such as reef fishes in San Diego, CA (Anderson et al. 1989). The mean body sizes of these fishes were highly dependent on microhabitat conditions such as substrate composition, with ecotone and sandy substrate correlated with larger body lengths. In this case, smaller fishes preferred rocky substrate due to cover necessity, less frequently occupying the more exposed ecotone and sandy region. Furthermore, numerical fish density was highest in rocky regions due to favorable feeding conditions. Thus, microhabitat conditions strongly affect both the distribution and body size of aquatic organisms. These factors in turn may alter trophic cascades by changing the function of top predators in top-down regulated ecosystems.

Another predator species that is affected by microhabitat composition is the coastal giant salamander, *Dicamptodon tenebrosus*. They inhabit Pacific northwest coastal riparian areas where creeks are relatively shallow, and therefore they are at the top of the aquatic food chain since there is not enough space nor resources to support predators of a larger size. In these creek ecosystems, *D. tenebrosus* larvae are top predators, consisting over 90% of predator biomass in many creeks (Parker 1994). Salamander larvae consume a variety of freshwater macroinvertebrates and fish hatchlings. Through their position at the top of the food web and their voracious diet, *D. tenebrosus* stabilizes the creek ecosystem through a trophic top-down control. Therefore, any changes in *D. tenebrosus* larvae populations can drastically alter the populations of other stream organisms. Like the whitetail dragonflies, *D. tenebrosus* is

cannibalistic, so larger salamander larvae can incorporate larger prey into their diet as they grow, such as the smaller larval *D. tenebrosus*. Thus, both the population density and the size of *D. tenebrosus* directly affects the population of their prey and may even affect the distribution of smaller *D. tenebrosus* larvae as they avoid predation by larger conspecifics. Therefore, although we do not yet know what factors affect salamander size, salamander size is likely to have a larger effect on the rest of the system.

The abiotic factors that affect *D. tenebrosus* have largely been studied in the context of effects on population density. Larval density is thought to be best predicted by microhabitat creek conditions such as substrate composition (Welsh and Lind 2002). Parker 1991 showed a strong positive correlation between loose rock availability and larvae abundance in Northern California, indicating that the density of rock cover was a limiting factor of *D. tenebrosus* abundance. Further, *D. tenebrosus* larvae may favor small, slow-moving streams (Welsh and Lind 2002). However, this pattern may not be consistent between streams, as slow-moving streams have higher silt deposition, a factor that is known to reduce salamander larval density (Ashton et al. 2006). Specifically, the deposition of fine sediment may create unsuitable habitats for amphibians, as it fills interstitial spaces between rock crevices and reduces overall habitat availability (Ashton et al. 2006). Furthermore, fine sediment also promotes the growth of microflora and mold harmful to salamander gill health, reducing population density (Lefcort et al. 1997). Thus, it may be that wider, faster-moving streams are preferred by *D. tenebrosus* larvae. Although studies like those above have determined some effects of abiotic

factors on density of *D. tenebrosus* larvae, no studies have examined the effect of abiotic factors on larval body size.

Based on creek conditions and population dynamics, *D. tenebrosus* body size may be affected by substrate composition or intraspecies interactions. For example, increased rock cover provides surface area for more macroinvertebrates (Davic and Orr 1987). Since salamander growth is indeterminate and growth rates depend on food availability, an increase in rock cover could indirectly provide *D. tenebrosus* larvae with more food and indirectly increase their body size (Bruce 2003). Furthermore, the potential for cannibalistic interactions may drive smaller individuals to avoid cohabitating in the same microhabitat as larger individuals, so they may be far less abundant in streams with larger larvae. This would decrease both the average body size and overall abundance of larvae, as any remaining smaller larvae are likely to be preyed upon by larger individuals. Based on this, we were interested in how differing microhabitat characteristics affect salamander body size and density within the same larger ecological system.

To further understand how creeks of differing size have distinct microhabitats and how that affect *D. tenebrosus* larval population density and size distribution in the same larger ecological setting, we studied three creeks within the Angelo Coast Range Reserve located in Mendocino County, California, USA. The three creeks are situated in the same old-growth forest, but each creek has a different drainage level and thus potentially distinct microhabitat caused by differing water flow bringing in varying substrates onto the creek bed (McNeely 2007). We hypothesize that in all creeks, as the density of cover rocks increases, *D.*

tenebrosus larval density also increases. Conversely, we predict that as the percentage of silt increases within a pool, larval density will decrease. Due to visually differing creek substrate composition, we hypothesize that larger creek will have a higher density of cover rocks, a lower amount of silt, higher salamander larval density, and larger salamander larvae, whereas smaller creek will have a lower density of cover rocks, higher amount of silt, lower salamander larval density, and smaller salamander larvae. Furthermore, the presence of a large *D. tenebrosus* larvae within a pool will have a positive effect on the mean body size of other *D. tenebrosus* larvae.

METHODS

2.1 Natural History

Coastal giant salamanders (*Dicamptodon tenebrosus*) are native to the coastal regions of British Columbia, Oregon, Washington, and northern California (Stebbins and McGinnis 2012). Here, they feed on invertebrates and other unusual prey items such as small snakes, shrews, young rodents, and their own kind. These amphibians prefer temperate regions of fresh flowing water within forested communities.

To survey *D. tenebrosus*, freshwater pools were studied within the area of UC Angelo Coast Range Reserve, CA, USA from August 1st to August 5th, 2023. Angelo Reserve is situated in an expansive old-growth forest in Mendocino County. The area harbors a multitude of terrestrial and aquatic habitats, including redwood groves, mixed conifer-deciduous forests, salmon-barring mainstream rivers, and tributary streams (“Natural History – Angelo Coast Range

Reserve” n.d.). The creeks of Angelo Reserve include Fox Creek, McKinley Creek, and Elder Creek, all of which are tributaries of the South Fork Eel River.

During periods of low flow (April through November), the creek channels consist of wide, shallow pools connected by short riffles (Parker 1991). These conditions allow for a wide range of aquatic larval organisms such as mayflies, stoneflies, hellgrammites, caddisflies, and damselflies; all of which are included in the diet of *D. tenebrosus*.

Observationally, Fox Creek is characterized by medium flow rates, a drainage area and a greater abundance of gravel, McKinley Creek by slow-moving water and greater levels of silt, and Elder Creek by fast-moving water and levels of rock and gravel similar to Fox Creek. With drainage areas used as a proxy for water flow and thus size, McKinley Creek is a small creek with a drainage area (DA) of 0.58 km², Fox Creek is a medium-sized creek with a DA of 2.8 km², and Elder Creek is a large creek with a DA of 13.5 km² (McNeely and Power 2007, Schade et al. 2011).

2.2 Pool Selection and Characteristics

To survey this system, we examined 20 pools from all three creeks (Fox Creek, McKinley Creek, and Elder Creek). Pools were defined as bodies of slow or stagnant water that were bound by exposed rocks. The length and width of surveyed pools were restricted to 0.5 to 2 m, and the depth was restricted to a maximum of 35 cm for the sake of convenience and accuracy, as pools any larger than these parameters would increase the number of inaccessible larvae in rocks or sediment. To determine the surface area of each pool, the longest length and width were measured in meters. The formula for the area of an oval was used to

determine the area of each pool. To understand pool-level sediment characteristics of the *D. tenebrosus* microhabitat, we conducted a percent visual estimate in which the percent visual estimate for rocks and silt was taken by each member and then averaged amongst the group. We collected data moving upstream to prevent interference with other study pools via substrate dislodgement or salamander displacement.

2.3 *Dicamptodon tenebrosus* Survey Method

A total of 80 salamanders were surveyed from Fox, McKinley, and Elder Creek. The collection of *D. tenebrosus* larvae started with an initial survey of the pool to locate individuals out in the open. After the collection of these initial larvae with aquarium nets, rocks were removed and placed to the side of the pool before another larvae observation was conducted. Per Parker 1991, we counted all unembedded rocks over 7.5 centimeters to measure rock cover density. Rock density was calculated by dividing the number of rocks by the pool's area. Before leaving the pool, one last examination was done by inserting hands beneath the pool's rock, gravel, and silt to flush out any remaining larvae.

Observed *D. tenebrosus* were transferred to a dipnet placed in sections of the creek adjacent to the focal pool to avoid double counting and to conduct individual measurements. In the dip net, snout-to-vent length (SVL) was measured to the nearest centimeter. After a maximum observation period of 25 minutes, we counted the total number of larvae collected and placed them and the rock back in their original positions. *D. tenebrosus* larval density was calculated

by dividing the number of larvae by that pool's area.

2.4 Analysis

All statistical analyses were conducted using JMP statistical software v17 (SAS institute inc., Cary, NC, 1989–2023). Linear regression was used to test if rock density affected *D. tenebrosus* larval density. Another linear regression was used to determine if the amount of silt in each pool affected the density of *D. tenebrosus* larvae. Then, to analyze a difference in abiotic factors between creeks, an ANOVA was used to look at the visual percent cover of silt among all three creeks. ANOVA was again used to test differences in salamander larva density and SVL between Fox, McKinley, and Elder Creek.

RESULTS

As the number of rocks over 7.5 cm per m² increased, the number of *D. tenebrosus* per m² in a pool also increased ($N = 60$, $r^2 = 0.34$, $p < 0.0001$; Fig. 1). However, there was no relationship found between the number of *D. tenebrosus* per m² and the percentage of silt cover in a pool ($N = 60$, $r^2 = 0.0004$, $p = 0.88$).

The large creek had a marginally higher percent cover of rocks compared to the medium and small creeks ($N_{\text{small}} = 20$, $N_{\text{medium}} = 20$, $N_{\text{large}} = 20$, $F = 2.64$, $p = 0.08$); the small creek had a higher percentage cover of silt compared to medium and large creek ($N_{\text{small}} = 20$, $N_{\text{medium}} = 20$, $N_{\text{large}} = 20$, $F = 18.93$, $p < 0.0001$). However, there was no difference in *D. tenebrosus* larval density between the three creeks ($N = 60$, $F = 0.07$, $p = 0.93$).

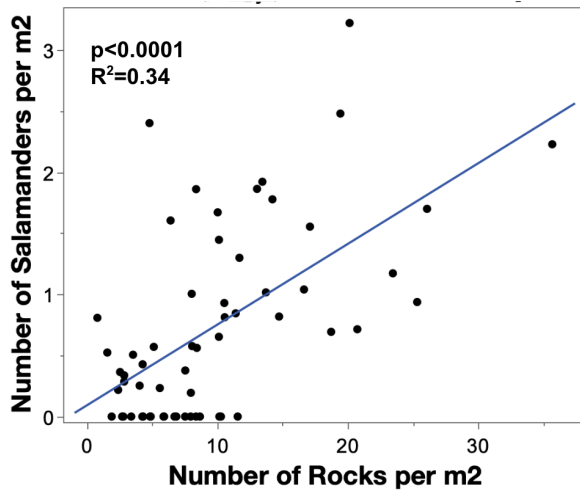


Figure 1: Relationship between the number of *D. tenebrosus* in a pool per m² and number of rocks in a pool per m². Study was conducted within Angelo Coast Reserve CA, USA, from August 1–5, 2023. A linear regression test was used to analyze the relationship between the number of *D. tenebrosus* in a pool per m² and number of rocks in a pool per m². The number of rocks was counted by removing and counting every unembedded rock over 7.5 cm in the pool. The number of *D. tenebrosus* was also counted. Rocks per m² and *D. tenebrosus* per m² were calculated by dividing the total number of rocks and *D. tenebrosus* by the area of the pool. Data points represent salamander density (individuals/m²) and rock density (rocks/m²) in each of the 60 pools. (N = 60, r² = 0.34, p < 0.0001).

D. tenebrosus larvae in the small creek had a significantly smaller SVL compared to *D. tenebrosus* in the medium and large creeks (N_{small} = 32, N_{medium} = 30, N_{large} = 19, F = 9.56, p = 0.0002; Fig. 2). The presence of a large *D. tenebrosus* in a pool had a marginally positive effect on the mean SVL of the remaining *D. tenebrosus* in the same pool (N = 38, t = 2.09, p = 0.055; Fig. 3).

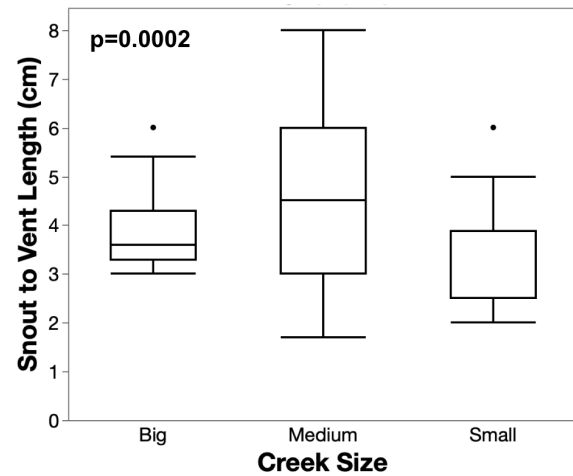


Figure 2: Comparison of snout to vent length (SVL) in centimeters across three creeks. Study was conducted within Angelo Coast Reserve CA, USA, from August 1–5, 2023. We used ANOVA to determine differences in mean SVL between Large, medium, and small creeks in Angelo Coast Range Reserve located in Mendocino County, California. Snout to vent length (SVL) was measured as the distance, in centimeters, from the tip of the snout to the most posterior opening of the cloaca from the dorsal side of *D. tenebrosus*. The whiskers at the top and bottom of the plot represent the maximum and minimum values of SVL in that creek, respectively. The dots represent outliers. The 25% quantile, median, and 75% quantile are represented by the horizontal lines in each boxplot from bottom to top. There was a difference between the SVL of *D. tenebrosus* in small Creek compared to the SVL of *D. tenebrosus* in medium and large Creek (N_{medium} = 30, N_{small} = 32, N_{large} = 19, F = 9.56, p = 0.0002).

DISCUSSION

We found support for our hypothesis that a higher density of cover rocks would result in an increase of larval *D. tenebrosus* density across all creeks, however contrary to our hypothesis there was no difference in rock density between the creeks of different speeds. Unlike our hypothesis we also found no correlation between larval *D. tenebrosus* density and visual percent silt, yet there was more silt in small creek than in medium

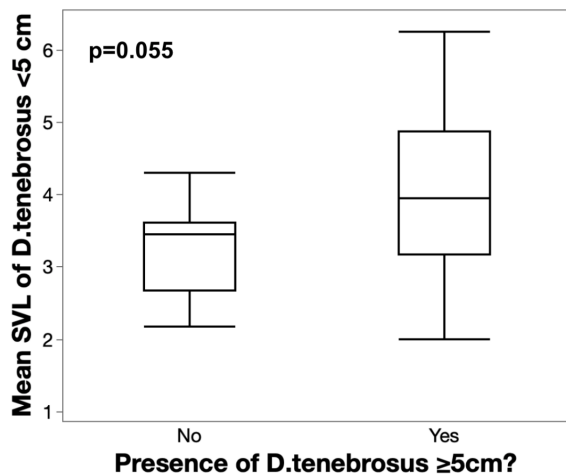


Figure 3: The effect of presence of an individual ≥ 5 cm on the mean SVL of the rest of *D. tenebrosus* in the pool. Study was conducted within Angelo Coast Reserve CA, USA, from August 1–5, 2023. A t-test was utilized to understand how the presence of *D. tenebrosus* individuals affected the mean SVL of the remaining individuals within that same pool. We analyzed *D. tenebrosus* which has an SVL at or over 5 cm as a large individual and categorized all the pools as “yes” or “no” based on the presence or absence of an individual at this site. Then, we removed the large individual and calculated the mean SVL for the remaining *D. tenebrosus* in the pool. There is a marginally significant difference between groups, and with the presence of a large individual, the mean SVL is likely higher for the rest of *D. tenebrosus* in the same pool (N = 38, t = 2.09, p = 0.055).

creek and large creek. We also found support for our hypothesis that the larvae caught in small creek were significantly smaller than both large creek and medium Creek, which could be correlated to stream size due to a variety of reasons. However, our results differed from expectations in how there was no size difference between large creek and medium creek, despite a slightly different creek size, implying that their water flow rates are not as distinct as we initially predicted.

Across all creeks, *D. tenebrosus* larvae had a higher density in pools with more unimbedded rocks, which confirms previous

findings that suggest larvae prefer areas with more objects that can provide cover (Parker 1991). Additionally, some studies have found that greater rock coverage provides more surface area for aquatic macroinvertebrates, which is a large part of the diet of *D. tenebrosus* (Davic 1983, Davic 1987). Not only do rocks provide possible protection, but they also are a habitat for the main food source of salamander larvae. We did not find any difference in the rock density between separate creeks with differing water flows. This could be because rock cover does not vary with creek flow, whereas factors like silt cover are carried and washed away by increases in water flow.

An increase in silt is often characterized by creeks with slower creek flow rates and a reduced amount of water, making the size of streams an important factor in our study system. We found that the slowest-moving creek had the highest abundance of silt as well as the smallest overall salamander size. However, we also found no significant correlation between larval salamander density and the presence of silt. This is contrary to our initial predictions, as previous research has shown that silt has a negative impact on salamander health (Lefcort et al. 1997). Although *D. tenebrosus* larval population density did not decrease in the presence of silt, the presence of silt correlated with a decrease in larval body size. Salamander larval size and silt abundance have not been linked before, so future studies could examine this relationship further with different concentrations of silt. It has been suggested by recent experiments with similar salamander densities that the salamanders could be using the silt to burrow into for cover as an alternative to using rocks (Neal 2022). This suggests a possible positive

relationship between silt cover and larval salamander density. Furthermore, it was more difficult to collect salamanders in pools containing silt because slight disturbances stirred up sediments and reduced visibility, which could be a desirable anti-predator microhabitat trait for larvae. Although larvae of *D. tenebrosus* did not show any differences in density between the pools containing silt, this could be explained by the ways both silt and rock can provide hiding opportunities.

Like silt, abundance of macroinvertebrates is also affected by creek size. Faster-moving water means more invertebrate movement between pools as well as more available invertebrate habitat space (Davic and Orr 1987). Furthermore, in flood years, when water is most abundant, salamanders have twice the amount of food in their stomachs than in non-flood years (Petranka 1986). Since having more available food is known to result in salamander larvae growing faster and metamorphosing sooner, increased water flow could contribute to higher larval body size (Beachy 1995). This could explain why the medium and large creeks have larger salamander larvae, since they have faster-moving water than the small creek. It follows that the larvae within the large and medium creeks may be growing larger and metamorphosing sooner due to the increase in food abundance delivered by faster-moving water.

Other factors could also be affecting *D. tenebrosus* larval size. Contrary to our results, past studies have found that as larval salamander density increases, salamander size decreases due to competition (Petranka 1986). The low water flow in small Creek means that pools were much farther apart and separated by land rather than by wide areas of moving water through which larvae

could move between pools. So, although we found that larval salamander density was approximately equal across all three creeks, the physical characteristics of the low-flow creek may limit travel for both salamanders and the influx of food sources, condensing the larvae population into fewer pools. Therefore, it is possible that *D. tenebrosus* larvae are competing much more in the low-flow creeks than in larger creeks. A study on artificially isolated crayfish found that high density populations depleted resources and experienced reduced growth rates (Abrahamsson 1966). Increased *D. tenebrosus* larval interaction within pools of the slow-moving creek could account for the smaller overall size of larvae since both resources and space are restricted within this system. A future experiment that isolates pools from new resources and salamander pool-hopping could investigate further the effect of pool isolation on salamander size.

Our results show that across all the creeks, the presence of a large salamander may be an indicator of larger overall salamander size in the surrounding pool. This could be because large salamander larvae are known to be cannibalistic towards smaller larvae (Kusano et al. 1985). Large *D. tenebrosus* larvae may either be eating all the smaller larvae in the immediate vicinity, or the smaller larvae could be avoiding them, meaning that the only larvae that inhabit the same area are those that are too large to consume. In this way, salamander larval size affects trophic dynamics, as the smaller salamanders being eaten are going down a trophic level.

Understanding what substrate is preferred and thus which creeks are more suitable for salamanders can help us understand how abiotic factors, such as the composition of

substrate that make up a microhabitat, affect their population density and size. Changes in salamander population density and size demographics in turn impact the feeding behavior of salamander larvae, changing macroinvertebrate and fish hatchlings' abundance, therefore having a cascading effect on plant materials and algae that these macroinvertebrates and fishes feed on. Trophic relationships work on a delicate balance. Any changes in higher trophic level are going to have cascading effects on lower trophic levels. For this reason, salamander larvae population is important to consider when making conservation decisions regarding species in lower trophic levels, as well as knowing how conservation of salamander populations affects their prey and beyond. Given the strong influence of microhabitat conditions on the function of this top predator in the creek ecosystem, habitat conservation must consider maintenance of small-scale abiotic factors, such as substrate composition of creek beds.

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