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Abstract approved:

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Identifying the patterns and drivers of movement is critical for understanding species biology, population dynamics, and community ecology. Movement of co-dominant fish and salamander species has never been studied concurrently in lotic environments despite their importance as vertebrate predators. We conducted a mark-recapture survey of cutthroat trout (*Oncoryhnchus clarkii*) and Pacific giant salamanders (*Dicamptodon tenebrosus*) in two reaches of a 3rd order headwater stream to determine movement patterns during summer. We also conducted biomass and abundance surveys at four sites along the 2km stream to learn how the species composition of these two co-dominant vertebrates changes along a stream gradient. We found that *D. tenebrosus* show a distinct upstream movement bias while *O. clarkii* are generally immobile during summer low flow. We also found that length is significantly correlated to movement for *D. tenebrosus.* Additionally, along a stream gradient, biomass/m² is relatively constant and similar for both *D. tenebrosus* and *O. clarkii*.

Keywords: Dicamptodon tenebrosus, Oncoryhnchus clarkii, cutthroat trout, Pacific giant salamander, movement, season

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Summertime movement, biomass, and abundance of co-dominant cutthroat trout and Pacific

giant salamanders in Cascade Mountain headwater streams

by

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I understand my project will become part of the permanent collect of Oregon State University, University Honors College, and will become part of the Scholars Archive collection for Fisheries and Wildlife. My signature below authorizes release of my project to any reader upon request.

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Introduction

Movement is an important process for both aquatic and terrestrial organisms, enhancing genetic variability (Angers & Bernatchez, 1995), facilitating population persistence (Avise, 1992), and promoting reproductive success (Bowler & Benton, 2005). Movement can vary spatially, ranging from local home range movements to large-scale global migrations, as well as temporally, including diel migrations (Hays, 2003; Bunnell et al. 1998) and seasonal movements (Webster et al. 2002, Block et al. 2001). Studying both spatial and temporal patterns of movement is critical for understanding individual behavior, population dynamics, and species distributions (Baird and Krueger 2003; Curry et al 2011; Mollenhauer et al 2013). Movement is inherently complex and difficult to study, often limiting the scope and significance of studies attempting to assess drivers of movement. By confining studies to well delineated spatial and temporal environments such as small headwater streams, we can likely distinguish drivers and patterns of movement for stream dwelling organisms such as fish and amphibians.

The majority of studies evaluating spatial and temporal movement in streams have largely focused on resident salmonid species as they are culturally and recreationally important. Originally described as sedentary (Gerking, 1959), the paradigm of restricted fish movement shifted in the mid-90s to a more complex concept of mixed populations and communities of mobile and sedentary fish (Gowan and Young, 1994). While the majority of resident stream fish are unlikely to move outside their home range, a substantial proportion of fish do move great distances (Young 1994; Swanberg 1997; Hilderbrand and Kershner 2000). For example, some brown trout in Michigan were observed moving over 30 km within a year, presumably in search of food (Clapp et al. 1990). The majority of populations are sedentary, however, with limited home ranges varying among fish species, habitat type, and stream size (Gowan and Young 1994; Young and Tonn 2011).

Temporal movements by trout vary regionally and are typically correlated with reproduction and changes in stream environment (Mellina et al. 2005; Young and Tonn 2011). Trout often become active during their spawning season and undertake large migrations to and from spawning grounds (Curry et al. 2002; Young 1996; Hilderbrand and Kershner 2000; Schmetterling and Adams 2004). Temporal variations in stream flow and temperature, particularly during summer, are also important drivers for fish habitat selection and movement (Swanberg 1997; Curry et al. 2002).

The spatial and temporal movement of salamander species in streams has received less attention than fish despite their importance as a vertebrate predator. Unlike fish that are strictly confined to movement within the active channel, some species of salamanders are capable of tolerating brief periods out of the water. Both local and broad scale terrestrial migrations regularly occur in amphibians. Trenham et al. (2001) found the California tiger salamander, *Ambystoma californiense*, travelled an average of 452m over land to locate new breeding ponds in Monterey County, California. In a study examining movement in the stream-dwelling salamander *Gyrinophilus porphyriticus*, Lowe and McPeek (2011) found that individuals moved over 500m in a $1st$ order stream. However, as with fish, the large majority of individuals in salamander population are generally not thought to make broadscale movements. Nearly 82% (n=417) of the terrestrial slimy salamander, *Plethodon glutinosus*, moved less that 9m in 9 months in an oak-hickory forest in North Carolina (Wells and Wells 1976). Movement in an aquatic population of wandering salamanders (*Aneides vagrans*) was less than 10m for 94.3% of a recaptured population from June to August (n=176) (Davis 2002). Ferguson (2000), additionally, found that Pacific giant salamanders (*Dicamptodon tenebrosus*) in a headwater stream in British Columbia moved an average of only 4m from July to October (n= 231).

Terrestrial and aquatic species of salamanders also exhibit seasonal movement patterns. For example, Madison (1997) found significant movement in spring and fall in pond-dwelling spotted salamanders, *Ambystoma maculatum*. Salamanders are also more active during the breeding season when they are travelling to and from breeding sites in ponds and streams (Kleeberger and Warner 1983, Douglas and Monroe 1981).

In many streams, salmonids and aquatic salamanders coexist as top predators. For example, cutthroat trout (*Oncoryhnchus clarkii*) and larval Pacific giant salamanders (*Dicamptodon tenebrosus*) are two common vertebrate predators in headwater streams of across the Pacific Northwest. Fish tend to occur in greater frequency in low-gradient mainstem rivers and salamanders tend to occur in greater frequency or in complete allopatry in high-gradient first-order streams (Murphy and Hall 1981), but they occur in similar frequencies and are co-dominant predators in mid- and low-order headwater streams (Murphy 1981). Although fish and salamanders often occupy the same habitat, compete for food resources (Sepulveda 2012; Parker 1994), and are dominant predators in headwater streams, their movement has not been studied concurrently.

We used mark-recapture methods to document movement of both fish and aquati salamanders together over a 6-week period in mid-summer 2013 in two of four study reaches. We hypothesized that movement would be correlated with body size and condition factor, and that there would be species-specific displays of upstream and downstream movement.

The second component of this study quantified the relative abundance and biomass of these two species along four sections of a 2 km long $2nd$ order headwater stream. This survey explored the trends in relative abundance and biomass of these two species at a large spatial scale (fifth to first-order) to determine the confines of their co-dominant range (i.e. within a single second-order stream). We hypothesized that the biomass of *D. tenebrosus* would increase relative to that of *O. clarkii* with increasing distance upstream from the tributaries' confluence with the mainstem stream.

Methods

Fig 1. Map of the HJ Andrews Experimental Forest. The black circles show the location of the 4 study sites along a 3rd order headwater stream.

Study site

This study was conducted in the H.J. Andrews Experimental Forest (HJAEF), a 6,400 ha National Science Foundation Long Term Ecological Research (LTER) forest, located on the west side of the Cascade Mountain range in north-central Oregon (44°12′44″N 122°15′20″W) (Fig. 1). The HJAEF is predominantly defined by the drainage basin of Lookout Creek, a 5th order steam. Lookout Creek has two primary sub-basins, the McRae Creek sub-basin and the upper Lookout Creek sub-basin. Elevations in these basins range from 354m where Lookout Creek enters Blue River Reservoir to 1630m at the top of

Carpenter Mountain. Climate in this region is Mediterranean with a dry summer season and a wet winter season (Fig 2).

The HJAEF has a patchwork of historic forest management activities beginning in the 1950s but the majority of the basin remains old-growth forest. Below 1000m, the old-growth forests are largely dominated by structurally complex stands of Douglas Fir (*Pseudotsuga menziezii*) and Western Hemlock (*Tsuga heterophylla*). Second growth stands, where present, are composed of relatively dense and uniform Douglas Fir forest. Forests above 1000m are composed of Mountain Hemlock (*Tsuga mertensiana)* and Pacific Silver Fir *(Abies amabilis)* (Franklin and Dyrness, 1988).

Fig 2. Annual discharge of Lookout Creek located on the HJAEF. The gray rectangle indicates the duration of the study.

We conducted our study on an unnamed $3rd$ order tributary of McRae Creek (hereafter McTrib) during summer low flow. The stream flows through riparian forests of 200-500 year-old old growth Douglas Fir and naturally regenerated second-growth stands of Douglas Fir cut in the 1950s. *O. clarkii* and *D. tenebrosus* are the only vertebrate species present in McTrib.

Surveys were conducted at four study reaches along the second-order section of McTrib. Site 1 was the furthest upstream, beginning at the confluence of three first-order streams downstream of plot 522, where McTrib becomes a second-order stream (Fig. 1). Reach 2 was located in plot L503, a 16.6 ha naturally regenerated second-growth stand of Douglas Fir cut in 1953. Reach 3 was located 100m downstream of plot L503, 1000m up from the confluence of McTrib with McRae. Reach 4 was the furthest downstream and was 200m from the confluence. Reaches 1, 3, and 4 were located in old-growth forest and Reach 2 was in second growth forest. Reach length varied depending on accessibility and habitat constraints.

Field methods

Vertebrates were sampled using multiple pass depletion methods with a Smith-Root LR-20b backpack electroshocker. Block nets were carefully placed across both the upstream and downstream ends of the reach to prevent vertebrate movement between passes. Three passes were completed in each reach to obtain sufficient depletion of both fish and salamanders.

O. clarkii were the only fish species present. All fish were anesthetized with Aqui-S 20E Fish Sedative (AquaTactics), measured to the nearest millimeter total length and weighed to the neared 0.1 gram. Fish over 60 mm were injected with a subcutaneous Visual Implant Elastomer (VIE) tag under their dorsal fin and behind their eye on their left side. Fish larger than 90mm also received a 9mm Passive Integrated Transponder (PIT) tag. *D. tenebrosus* was the only salamander species captured. We measured the snout vent length (SVL) and total length of all individuals to the nearest mm and weighed each salamander to the nearest 0.1g. All salamanders were injected with a VIE tag posterior to their left forelimb. All tagged individuals were placed in an aerated recovery unit containing antibacterial recovery agent until visually recuperated.

Habitat surveys

We conducted stream habitat surveys in each study reach. Surveys included quantification of large wood, bankfull and wetted widths, gradient, percent substrate, and pool area. Large wood, classified as pieces greater than 10cm diameter and 100cm length, was counted and the volume was calculated by measuring the length as well as the diameter at both ends. Ocular measurements of percent substrate within 2 meters of 10 randomly selected points were taken within each reach to identify dominant substrates. Pools were assessed by measuring residual depth, outflow depth, length, and width.

Movement

Movement was examined in the paired high-gradient low-gradient sites of Reaches 2 and 3 after 1 week for salamanders and after 6 weeks for both salamanders and fish. After

being PIT tagged, fish were reintroduced evenly into the respective reach from which they were captured. In each shocked reach, all tagged salamanders were released at a single location near the middle of the reach. Salamanders could not be individually identified and therefore, a single release point in the middle of each reach allowed us to quantify movement from a known location.

After 1 week, we re-shocked Reach 2 and 3 and marked the locations of individually tagged fish. All recaptured salamanders with elastomer tags were noted for length and location relative to the release point. This gave us salamander movement after a one-week interval. Salamanders were put back in the stream in the exact location from which they were recaptured. Only one pass was made in order to not conflict with a concurrent study involving young of the year cutthroat trout. We shocked Reaches 2 and 3 again 6 weeks after the $1st$ recapture to assess long-term summer movement for salamanders and fish. Tagged fish and salamanders were marked for location and then measured for length and weight. Two passes were made as this shocking event occurred after the aforementioned young of the year study was completed.

Data Analysis

Population estimates were made using the program MICROFISH by calculating the maximum likelihood estimation after multiple pass depletions. Biomass for each reach was then calculated by multiplying the maximum likelihood population estimate by the mean mass in each respective reach. Movement was attributed to any individual recaptured more than 1m away from the release point. Upstream movement was given positive values and downstream movement was given negative values. Daily movement was calculated by

dividing an individual's total movement by the daily interval between release and recapture. This allowed us to standardize movement over time for both *O. clarkii* and *D. tenebrosus*. Condition factor for *D. tenebrosus* was calculated using a length corrected weight (Lowe et al. 2006) and for *O. clarkii* was ln(L) / ln(W). Data was tested for normality using Kolmogorov-Smirnov normality test. We tested for normality in Site 3 after removing all *O. clarkii* that moved 0m from the analysis. We did not have enough recaptured individuals in Site 3 week one to run an analysis. We regressed condition factor and length with daily movement after 1 week of movement for *D. tenebrosus* and after 6 weeks for both *D. tenebrosus* and *O. clarkii*. A mark-recapture population estimate was not done in Reach 2 or 3 due to inconsistent effort between recapture 1 and recapture 2.

Results

We captured a total of 136 *O. clarkii* and 130 *D. tenebrosus* in the course of this study. We marked all *O. clarkii* >50mm in the middle two reaches with reach-specific elastomer tags and all individuals >90 mm (n=50) received individually identifiable PIT tags. We marked all *D. tenebrosus* (n=90) with reach-specific elastomer tags in the middle two reaches of our study stream. We recaptured 44% of the PIT tagged *O. clarkii* and 25.5% of the *D. tenebrosus.* PIT tag retention was high throughout the duration of the study.

Vertebrate biomass/ m^2 was lowest at the downstream reach and highest at the upstream site (Fig. 3). The two mid-elevation reaches had comparable vertebrate biomass/ m^2 , despite the difference in forest types, large wood, and pools (Fig. 1; Table 1). When considering total biomass, rather than biomass/ m^2 , we found biomass was lowest at Site 4 and highest in the mid-elevation high gradient Site 3.

The relative abundance of fish versus salamanders among these four sites ranged from 64% fish (36% salamanders) to 29% fish (71% salamanders). However, as with total biomass the relative abundance of fish was lowest at Site 4 and highest as Site 1. This result, which contrasts with our expectations, is attributable to the changes in fish biomass more so than changes in salamander biomass.

Fig 3. Biomass/m² of trout and salamanders relative to landscape position in the stream.

Condition factor of fish did not correlate significantly with movement for *O. clarkii*. Length was positively correlated to movement for *O. clarkii* but this relationship was not significant (Fig. 4). Both length and condition, however, were significantly correlated to *D. tenebrosus* movement in both Site 2 and Site 3 after 1 week and 6 weeks of movement (Table 2).

Fig 4. Movement/day after 1 week and after 6 weeks in low and high gradient sites.

In agreement with our hypothesis, *D. tenebrosus* showed a strong upstream bias. Of the 23 individuals recaptured in our study, 74% moved upstream, 17% stayed within 1 meter of the release point, and 9% moved downstream. Fish did not display any significant directional bias in movement. There was, however, a marked absence of upstream movement in fish $(n=5)$ (Fig. 5).

Fig. 5. Directional movement of fish and salamanders was attributed to any movement beyond 1m of the release point. Negative values were given to individuals recaptured downstream and positive values to individuals recaptured upstream.

Discussion

Few studies have attempted to describe concurrent movement in two co-dominant vertebrate species. In a $2nd$ order tributary in the Cascade Mountains, Oregon, we found distinct upstream movement in the larval Pacific Giant Salamander, *Dicamptodon tenebrosus*. Cutthroat trout, *Oncoryhnchus clarkii*, showed no striking display of directionally biased movement. There was, however, an interesting absence of upstream movement in *O. clarkii*. In an attempt to understand the drivers of movement in these two species, we assessed movement patterns relating individual characteristics such as length, weight, and condition for both *D. tenebrosus* and *O. clarkii*. We found that longer (total length) *D. tenebrosus* moved greater distances relative to shorter individuals, contrasting

with *O. clarkii,* which showed no pronounced movement relationship with the same individual characteristics. In addition to patterns of movement, when examining the relative biomass of *O. clarkii* and *D. tenebrosus* along the stream gradient, we found fairly constant D. tenebrosus biomass/m² throughout the stream, while *O. clarkii* biomass/m² increased as we sampled further upstream. The relative contribution of *D. tenebrosus* and *O. clarkii* to total vertebrate biomass/m2 was remarkably similar along the stream gradient as well, with the exception of the downstream site, Site 4, which had much lower biomass/ m^2 for O . *clarkii*.

In our study system *D. tenebrosus* and *O. clarkii* each displayed unique patterns of movement relative to each other as well as when compared to other studies documenting movement in these same species. Studies examining movement in aquatic salamanders have found varying degrees of directionally biased movement as well as relationships to length and condition. Biased upstream movement does appear to be relatively common for stream dependent salamander species (Grant 2010; Lowe 2008; Lowe et al 2006). Movement may be species specific or seasonally dependent, however, and is likely influenced by the life history of the species (Lowe 2008; Kleeberger and Werner 1983). For example, *G. porphyriticus* was found to distinctly move upstream while in the same stream *Eurycea bislineata* was found to move downstream (Lower 2008). Seasonality also may influence movement, as Douglas and Monroe (1981) and Kleeberger and Werner (1983) found directionally biased post breeding movement. Additionally, while we found summertime movement to be common in *D. tenebrosus,* Gregory (pers. comm.) found no net movement of this species on an annual basis, suggesting individuals move downstream at another time of the year.

Quantifying the motivation for movement and correlating environmental and physical variables to movement is difficult and has rarely been studied in stream salamanders. Movement is thought to be provoked by conditions that will lead to increased overall fitness (Gadgil 1971; Lowe and McPeek, 2011). Therefore, one or multiple factors that ultimately leads to increased fitness likely explain the upstream movement by *D. tenebrosus*. Lowe et al. (2006) found that biased upstream movement from a lower section of a stream by the salamander *G. porphyriticus* compensated for low reproduction in the upper section of a 1st order headwater stream. Additionally, Lowe and McPeek (2011) found that survival of *G. porphyriticus* increased with dispersal distance, suggesting mobile individuals have greater fitness. Ferguson (1998) found that size, condition, density, and biomass had no relationship to movement in *D. tenebrosus* in British Columbia, the northernmost range of this species.

Studies of *O. clarkii* movement have been much more comprehensive and well documented than those for *D. tenebrosus*. Overall, these studies have found upstream movement during spawning season (Young 1994; Mollenhauer 2013) and restricted movement during summer while flows are low (Curry 2002; Kahler 2001; Schrank and Rahel 2004). While we found no directionally biased movement and no relationship between movement and physical attributes for *O. clarkii*, we did see an interesting absence of upstream movement, contrasting substantially with significant upstream bias in *D. tenebrosus*.

As snowmelt dominated headwater streams are particularly responsive to environmental changes, it is unsurprising that the denizens in these systems are highly plastic in their behavior and ability to adapt to changing conditions. Temporal variability, therefore, likely plays a large role in fish behavior and movement, and to a lesser extent for

salamanders (Gowan and Fausch 2002). Salamanders are less dependent on high stream flows for movement and therefore are not as confined to the same flow regimes as fish. As stream flow decreases steadily throughout summer and early fall in the Pacific Northwest, stream pathways for movement decrease and often result in impassable barriers to fish, explaining the apparent absence of upstream movement (Kahler 2001). This would suggest fish movement in our system occurs primarily during the high flows in late autumn, winter, and spring. Numerous studies of stream salmonids have indeed documented peak movement in spring and early June (Hilderbrand and Kershner 2000; Mellina 2005; Young 1996) and restricted movement in summer (Schrank and Rahel 2004).

Many studies have found significant relationships between size and condition and movement in both fish and salamanders. In stream dwelling salmonids, larger individuals appear to move greater distances relative to smaller individuals (Young 1994; Swanberg 1997; Bunnell et al. 1998; Gowan and Fausch 2002). We, however, found no such relationship in *O. clarkii*. When examining salamander movement relative to size, our results suggest larger individuals move more than smaller individuals. Other studies have found a range of responses with some finding significant size relationships (Cecala et al. 2009; Sepulveda and Lowe 2011) and some finding no significant size relationships (Ferguson 1998; Lowe et al. 2006). While length and condition were highly correlated in our study (*O. clarkii;* p=0.884; *D. tenebrosus*, p=0.939), we speculate larger individuals are more capable of moving and accordingly focused on length as a driver of movement.

There were also interesting disparities in *D. tenebrosus* movement rates between the low gradient (4.3%) and high gradient (5.6%) reach, with higher rates of movement in the low gradient reach compared to the high gradient reach. The high rate of movement and the low number of recaptures ($n=3$) in the $2nd$ recapture event in the low gradient site suggest the majority of individuals in the low gradient site moved out of the reach over the duration of the study (Fig 4, a/b).

In the second part of our study, we found relative biomass/m2 of *D. tenebrosus* to be relatively constant at each site regardless of changes in *O. clarkii* biomass/ m^2 . Lowe and Bolger (2004) found salamanders were less abundant when trout were present, suggesting trout may limit salamander abundance. This result may indicate that *D. tenebrosus* are generally unaffected by the presence of *O. clarkii* along a $2nd$ order stream gradient. Niche partitioning may be a mechanism for co-existence for these species, but Sepulveda et al. (2012) found little niche partitioning between fish and salamanders. As salamander biomass generally is highest in headwater systems (Murphy et al. 1981) we expected salamander biomass to be highest and the uppermost site and trout biomass to be lowest at the uppermost site. However, we found relative biomass/ m^2 of *O. clarkii* to be highest at the upstream site with the smallest wetted width and lowest at the downstream site with the highest wetted width.

While many of the drivers of movement are unclear, this study shows distinct movement patterns between two co-dominant stream dwelling predators during summer. Because *D. tenebrosus* is not subjected to the same summer low flow confines as *O. clarkii*, it can move upstream and access habitat and resources restricted to *O. clarkii* during summer and early fall. This may give *D. tenebrosus* a seasonal competitive advantage over *O. clarkii*. When considering seasonal movement from a management perspective, we've shown that *O. clarkii* are unlikely to move during summer suggesting they may be vulnerable to anthropogenic alterations to stream systems such as culverts, which may inhibit movement

to spawning grounds or restrict gene flow to upper reaches of streams. Additionally, we observed higher rates of movement in large *D. tenebrosus* in low gradient systems compared to high gradient systems. In the event of localized stream extinctions from natural disturbances or human activities, we may expect to see variable recolonization rates depending on stream gradient and the size of individuals in the stream. The results from this study highlight the importance of maintaining and preserving stream corridors to facilitate movement of stream organisms.

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APPENDICES

APPENDIX A

Table 1. Stream habitat data for 4 study sites in a $2nd$ order tributary in the Oregon Cascade Mountains. Large wood (denoted LW) is any piece of wood >100cm in length and >10cm in diameter.

	Length	(%)	Site Reach Gradient Total LW Volume	# of $LW*100$	# of Pools	Mean Pool	Mean	Mean	Mean BankfullwettedResidual
	(m)		$\rm{m}^{3*}100m^{-1}$	m^{-1}		Area (m ²)	(m)	(m)	Pool Depth (cm)
Site $\mathbf{1}$	50	8.75	12.5	30.0	$\overline{\mathbf{4}}$	3.27 士 0.85	4.14 士 0.51	0.77 王 0.15	17.25 士 2.50
Site $\overline{2}$	100	4.32	15.9	24.2	5	5.03 士 1.36	3.37 士 0.31	1.54 王 0.13	21.80 王 3.99
Site $\overline{\mathbf{3}}$	100	5.64	183.5	62.5	11	4.94 士 0.97	4.07 士 0.32	1.77 士 0.25	31.27 王 4.74
Site $\overline{4}$	50	13	38.7	38.0	6	7.58 士 1.85	7.18 王 0.78	1.94 王 0.18	32.67 王 1.73

APPENDIX B

Table 2. Movement statistics for *D. tenebrosus* and *O. clarkii* movement in Site 2 and Site 3. (-) denotes no data is available or an analysis was not completed.

Site 3

APPENDIX C

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