



Loss of catchment-wide riparian forest cover is associated with reduced recruitment in a long-lived amphibian

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ABSTRACT

Land use alteration is recognized as a threat for many aquatic species, but demographic drivers of land use associated declines are poorly studied. We examined hellbender, *Cryptobranchus alleganiensis*, demography in six stream reaches stratified across a land use gradient to understand how land use might influence a long-lived species. We used robust-design surveys (2014–2015) to estimate abundance and demographic structure, and all captures recorded between 2007 and 2015 to estimate demographic rates. Catchment-wide riparian (CWR) forest predicted demography better than catchment or local riparian forest. Across space, sub-adult/adult abundance declined and demographic structure became increasingly skewed towards older adults as CWR forest declined. Demographic rates indicated sub-adults/adults were being lost from each reach at a similar rate and most populations remained stable over the period for which data were available (1–8 years per reach). Our findings suggest recruitment (via births, juvenile survival and/or immigration) of young age classes facilitated stability of high-density populations when CWR forest was relatively high. When CWR forest was lower, survivorship and longevity of old adults facilitated persistence of low-density populations for multiple years while recruitment of young age classes suffered. Fine sediment was not correlated with land use but water temperature, conductivity and pH declined as CWR forest increased, highlighting water quality as a possible mechanism linking forest cover to hellbender demography. Our findings suggest maintaining forest in upstream riparian areas is critical for conserving downstream biota, and emphasize the difficulty of detecting declines in long-lived species when environmental alterations act specifically on recruitment of young age classes.

1. Introduction

Identifying factors that influence the abundance and distribution of species is fundamental to effective conservation planning. Freshwater fauna rank among the most threatened on Earth, largely as a result of rapid environmental changes caused by humans (Dudgeon et al., 2006). Habitat degradation as a result of surrounding land use alteration is recognized as one of the greatest threats to freshwater biodiversity at a global scale (Sala et al., 2000). While numerous species are known to respond negatively to increases in human land use intensity (Dudgeon et al., 2006), few studies have attempted to investigate the demographic mechanisms responsible for declines associated with land use (Österling and Högberg, 2014). That is, for most species, we know little about whether land use associated declines are driven primarily by insufficient recruitment (births, juvenile survival, and/or immigration) and/or excessive losses (deaths and/or emigration).

Building a more mechanistic understanding of how environmental alterations influence the abundance and persistence of species can

benefit conservation planning in multiple ways. First, demographic studies can highlight the relative benefit of conserving adult age classes versus improving survivorship of immature age classes when goals are to bolster wild populations. For example, research has highlighted the importance of maintaining high adult survivorship and/or immigration rates to ensure persistence of some turtles (Congdon et al., 1994) and pond-breeding amphibians that experience high variance in annual reproductive success as a result of environmental stochasticity (Taylor et al., 2006). Second, understanding how demographic rates respond to environmental alteration can highlight important factors to consider during monitoring. Monitoring efforts are often designed to provide early warning of declines that threaten population persistence. While focusing monitoring efforts on any age class might be appropriate for species with short generation times (Carginan and Villiard, 2002), biologically relevant shifts in the abundance of young age classes may take several years before culminating in a measurable change in adult abundance for slower paced life history strategists. Identifying the sensitivity of specific demographic rates to environmental change can

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thus facilitate earlier detection of population declines and development of more effective conservation strategies.

In the current study, we investigated associations between land use, in-stream habitat alteration and demography of a fully aquatic, long-lived, stream dwelling salamander of increasing conservation concern (USFWS, 2011a, 2011b). The hellbender, *Cryptobranchus alleganiensis*, is a large (up to 74 cm), benthic amphibian with a slow-paced life history strategy (Peterson et al., 1988; Taber et al., 1975). Their high degree of habitat specialization and apparent sensitivity to anthropogenic disturbance make hellbenders a likely umbrella species for stream ecosystems throughout their range. Hellbenders have experienced enigmatic, range-wide, precipitous declines since the 1970s and 1980s (Burgmeier et al., 2011; Foster et al., 2009; Graham et al., 2011; Wheeler et al., 2003). Other extant members of Family Cryptobranchidae include the Japanese giant salamander, *Andrias japonicus*, and Chinese giant salamander, *A. davidianus*, which share similar habitat requirements and life history traits with hellbenders and are also threatened with extinction (Ota, 2000; Wang et al., 2004). Cryptobranchid declines are widely suspected to be the result of habitat loss as a result of land use alteration and an associated increase in fine sediment loads (i.e., sand, gravel and clay that fill interstitial space; Sutherland et al., 2002) and decrease in water quality (Briggler et al., 2007; Okada et al., 2008; Wang et al., 2004). However, efforts to explicitly quantify the effects of land use on Cryptobranchid demography are lacking.

The overarching goal of our study was to better understand the demographic mechanisms through which land use might influence hellbenders. Our specific objectives were to 1) investigate associations between land use and demography (abundance, demographic structure and demographic rates) of local hellbender populations and between land use and in-stream abiotic conditions; and 2) quantify the relative strength of associations between land use within three spatial extents (catchment, catchment-wide riparian area, local-riparian area) and demographic responses. Our second objective was included largely because of variation in the spatial extent of land found to be most closely associated with demography of stream biota (see Willson and Dorcas, 2003). We predicted that local hellbender abundance would decline, demographic structure would become skewed towards older individuals (similar to patterns described by Okada et al., 2008; Wheeler et al., 2003), and that apparent survival (Φ) and population growth rates (λ) would decline as forest cover declined in surrounding areas. We predicted that water quality would decline, fine sediment (particles < 4 mm) would increase, and the proportion of boulders with cavities would decline as forest cover declined in surrounding areas, based on well established relationships between landscapes and in-stream habitat quality (Allan, 2004). We predicted that abiotic and biotic responses would be more closely associated with the extent of land we defined as the catchment-wide riparian area (collective riparian area throughout the upstream catchment) than with land use in the local riparian area or entire catchment, based on recent work highlighting broad scale measures of riparian condition as the most reliable predictor of in-stream ecological response (Stanfield and Kilgour, 2013).

2. Material and methods

2.1. Species background

The hellbender is a fully aquatic salamander, typically associated with cool, highly oxygenated and swift flowing stream habitat. Adults (290–740 mm total length) rely heavily on rocky crevices beneath large boulders and bedrock for shelter and nest sites (Nickerson and Mays, 1973). Sub-adults and adults show extremely high site fidelity to stream reaches and specific cavities within them (Bodinof et al., 2012a). Hellbenders exhibit longevity of 25+ years (Taber et al., 1975) and delayed maturity (5–8 year; Peterson et al., 1988)). Reproductive and

larval ecology is poorly understood. Spawning occurs annually during a brief (~14 d) period in early autumn, when members of both sexes congregate in and around potential nest cavities that are aggressively defended by a single male (Smith, 1907). Fertilization is external and males that are successful in attracting mates provide parental care for clutches of 100–1000+ eggs (Topping and Ingersol, 1981). Larvae measure 50–120 mm in length and use habitat ranging from deep gravel beds (Nickerson et al., 2003) to interstitial space among cobble and boulder substrate (Hecht-Kardasz, 2011). Following metamorphosis (~18 months, characterized by external gill resorption) hellbenders rely primarily on cutaneous respiration (Guimond and Hutchison, 1973) and have rarely been observed out of water (Coe et al., 2016). Little is known regarding hellbender tolerance to water quality parameters.

2.2. Study sites

Our study took place in a portion of the upper Tennessee River basin in southwest Virginia that encompasses portions of both the Blue Ridge and Ridge and Valley physiographic provinces. We studied hellbenders in six stream reaches (hereafter, R1-R6) staggered among three streams ($n = 1-4$ reaches per stream). The catchment upstream of R5 fell predominantly in the Ridge and Valley (98%) while the majority of catchments upstream of other reaches fell predominantly within the Blue Ridge (range = 66–100%). We selected stream reaches where we knew hellbenders occurred that were also stratified across a relatively wide gradient of catchment land use (Table 1) and reflected the approximate range of land use conditions to which hellbenders are exposed in Virginia (Bodinof Jachowski et al., 2016). Average wetted width of each reach ranged from 13 to 18 m. We defined length (range = 93–129 m) of each reach such that the extent of wetted stream channel was equal (~1680 m²) among reaches, thus facilitating comparison of hellbender abundance estimates. Due to the sensitive status of our focal species and threats of illegal collection we do not refer to waterbodies by name.

2.3. Quantifying land use

We considered human land use within the local riparian area, the catchment-wide riparian area and throughout the upstream catchment as a whole (Fig. 1). We use ‘riparian area’ to refer to the 50 m terrestrial corridor along each side of a stream (i.e., 100 m wide in total). Local riparian areas extended 1000 m upstream of a sampling reach (Fig. 1A) while catchment-wide riparian areas included the collective extent of riparian area surrounding all upstream tributaries (Fig. 1B); where tributaries included streams delineated in the National Hydrography Dataset (NHD) Plus version 2.1 (1:100,000 scale; USGS and USEPA, 2012). Catchments included all land within the contributing area upstream of a sampling reach (Fig. 1C). We used ArcMap version 10.1 (Esri, Redlands, CA) to delineate catchments and quantify the percent of each land use type within each spatial extent. We classified land use as forest (deciduous, evergreen, mixed forest and shrub and brush), agriculture (crop and grassland), low-intensity development (< 50% impervious surface) or medium-high intensity development (50–100% impervious surface) based on the 2011 national land cover database (NLCD; USGS, 2014)). For simplicity, we used percent forest as a univariate proxy of land use in each extent (hereafter, LR, CWR or C forest for local riparian, catchment-wide riparian and catchment areas, respectively). Due to concerns that the NLCD might underestimate forest cover in small spatial extents (Nowak and Greenfield, 2010), we validated our estimates of CWR and LR forest cover by visually generating 100 random points within polygons representing each spatial extent, overlaying points onto high resolution (0.3 m) aerial imagery, and visually classifying locations of points as either forest or non-forest. On average, percent forest cover estimated with the NLCD differed from the percent of points located in forest by only $-0.75\% \pm 2.17\%$ SE; thus we concluded that our NLCD estimates of forest cover were

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