Survival and Growth of Larval Coastal Giant Salamanders (Dicamptodon tenebrosus) in Streams in the Oregon Coast Range

Author(s): Jina P. Sagar, Deanna H. Olson and Richard A. Schmitz

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JINA P. SAGAR, DEANNA H. OLSON, AND RICHARD A. SCHMITZ

Conditions that affect amphibian larval growth and survival can affect population structure through both larval and adult stages of their life history. We conducted a two-year, mark-recapture study of larval, Coastal Giant Salamanders, *Dicamptodon tenebrosus*, in 14 small streams in the Oregon Coast Range to assess spatial and temporal variation in growth and apparent survival. We modeled larval survival and growth by season and age class and examined these demographic rates in the presence of road crossing culverts. Cormack-Jolly-Seber models indicated that apparent survival was lower for first-year larvae than second/third-year larvae (13%, SE = 0.03; 28%, SE = 0.08) and apparent survival varied by time/season. The >5% difference in the effect of age on survival is potentially biologically significant (effect size = −0.10; confidence interval = −0.05, −0.16). Effects of culverts on larval survival were inconclusive, while no effects on growth were detected.

FOR amphibians with complex life histories, populations may be regulated by mortality in each life history stage, from egg to adult (Wilbur, 1980). Selection pressures on each stage vary because larvae and adults of the same species may occupy different habitats. For many aquatic-breeding animals, life history stages exist as if independent of each other, yet aquatic conditions during the larval stage can influence adult morphology and fitness. In pond-breeding amphibians, larval conditions can affect size at metamorphosis (Wilbur and Collins, 1973; Wilbur, 1980), rates of metamorphosis (Shrode, 1972), adult fecundity (Scott, 1994), and adult fitness (Semlitsch et al., 1988). Conditions that affect larval growth and survival can affect population structure through both larval and adult stages of their life history.

Information on larval growth, survival, and population structure is particularly sparse for stream-breeding amphibians. The Coastal Giant Salamander, *Dicamptodon tenebrosus*, breeds in streams and is a dominant member of stream-community assemblages throughout the Pacific Northwest (Hawkins et al., 1983; Corn and Bury, 1989; Parker, 1994). Primary predators of larval *D. tenebrosus* are conspecifics and larger salmonids (Parker, 1993). Some life history variation by life stage is known for *D. tenebrosus*; for example, larval stage lengths can vary with latitude (Ferguson, 1998). The lotic larval period for *D. tenebrosus* in Oregon is estimated to be two to three years, at which point larvae either metamorphose into terrestrial adults or become paedomorphic aquatic adults (Nussbaum and Clothier, 1973). Environmental conditions, including those affecting growth and survival, may drive morphological adaptations of the larval and adult forms of this species in addition to population structure.

Both natural and anthropogenic disturbances can alter in-stream environments (Waters, 1995) and hence affect Coastal Giant Salamander growth, survival, and populations. Locally, roads and their associated culverts may influence a variety of physical stream processes such as suspended sediment load transport and water velocity, and culverts may directly affect in-stream organism movement (Warren and Pardew, 1998; Sagar, 2004), but the effect of culverts on the survival, growth and populations of larval stream salamanders are not known.

Environmental conditions also may affect amphibian sampling efficiency, an important consideration during population studies. Stream amphibians are difficult to sample (Richardson and Neill, 1998), and studies that rely on simple return rates (the proportion of marked animals released on one occasion and recaptured in the next occasion) to estimate survival may be biased (Lebreton et al., 1992, 1993; Martin et al., 1995). Use of return rates for estimating survival does not account for the probability of recapture (the probability that a salamander will be recaptured or resighted in a given capture occasion, if it is still alive and in the sample area; White and Burnham, 1999), and can result in a negatively biased survival estimator if capture rates are less than 1.0 (Lebreton et al., 1993; Martin et al., 1995).

The purpose of this study was to estimate the variation in growth and survival that occurs during the larval stage of *D. tenebrosus*. We used mark-recapture models to estimate rates of apparent survival and growth for two different larval age classes (first-year and second/third-

year), in summer and non-summer seasons and in the presence of culverts.

MATERIALS AND METHODS

We conducted our study in the central Oregon Coast Range on private timber lands and U.S. federal lands administered by the Coos Bay District of the Bureau of Land Management (BLM; Fig. 1). The study area lies in the Coast Range physiographic province, which is characterized by mild temperatures that range between 4.4 and 15.0 C and precipitation that falls mainly as rain between the months of October and March (United States Department of Interior, 2002). The forested slopes consist primarily of western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*), and riparian areas are dominated by red alder (*Alnus rubra*; Franklin and Dyrness, 1973). Road densities in the study area (varying from a low of 3.3 to a high of 6.2 km per road/km²; http://www.inforain.org/coqatlas/Road.htm), associated primarily with forest management activities, are comparable to stream densities (3.8 km per stream/km²; http://www.inforain.org/coqatlas/Subbasin.htm).

We restricted our site selection criteria to small, rocky, low-gradient, perennial stream reaches in the study area in which we found larval *D. tenebrosus*. We applied these selection criteria to a database of known culvert sites from the Coos Bay BLM and mapped road/stream intersections ($n = 81$). Study sites with a culvert (culvert site, $n = 9$) and without a culvert (reference site, $n = 5$) that matched the stream criteria above were selected for surveys. The sites were not selected randomly; however, all sites that matched the selection criteria were chosen to be sampled. The scope of inference is limited to the streams in this study.

Larval *D. tenebrosus* surveys were conducted during the summers 2002 and 2003 on reaches approximately 80 m in length for both culvert and reference sites. We designated the sampling areas on culvert sites such that a culvert was located at the center of the reach. Each stream was visited on five capture occasions (June, July, August 2002, and June, July 2003). We moved in an upstream direction and captured larval *D. tenebrosus* in small nets by systematically searching all wetted stream substrates in stream and culvert sections.

Captured larvae were measured (snout-vent length, SVL) and individually marked with visible fluorescent elastomer (Northwest Marine Technology, Inc.) at three body locations and released to their original capture site (Sagar, 2004). We had no known mortality from our handling.

Marking occurred on only the first two of five capture occasions due to limited resources.

Analysis.—Apparent annual survival and recapture probabilities were estimated using Cormack-Jolly-Seber (CJS) models in program MARK (White and Burnham, 1999) for larval *D. tenebrosus* in the Oregon Coast Range. Survival estimates in CJS models do not distinguish between death and permanent emigration and are therefore minimum estimates of true survival (Lebreton et al., 1993). However, movement distances for larvae were generally small throughout the study (80% of movements < 30 m; Sagar, 2004) and suggested low emigration rates. Permanent emigration of metamorphosing second/third-year salamanders could not be quantified and may bias survival estimates low for this age group. Analysis structure consisted of five capture occasions and four groups based on age class and stream type: reference stream first-year individuals; reference stream second/third-year individuals; culvert stream first-year individuals; culvert stream second/third-year individuals. Time intervals between capture occasions were unequal with two intervals (one month) in the summer 2002, one non-summer interval (ten months), and a single interval (one month) in summer 2003. We accounted for these uneven intervals in MARK. Using MARK, we examined whether there were differences in apparent survival or recapture probabilities that were associated with season (summer, non-summer), age class (first or second/third year), or culvert presence (culvert or reference stream).

We fit a fully parameterized global model that included a salamander age/culvert interaction with time effects and tested the goodness-of-fit of this model to the assumptions of the CJS model. We used the combined χ^2 (chi square) values and degrees of freedom (df) from Test 2 and Test 3 from the program RELEASE (Burnham et al., 1987) to estimate over-dispersion ($\hat{c} = \chi^2/df$; White, 2002) and test goodness-of-fit (Lebreton et al., 1992). We examined the chi-square tests and recapture matrix to determine in which capture occasion the overdispersion occurred. Overdispersion in the data often indicates a lack of independence or individual heterogeneity and occurs when the sampling variance is greater than the theoretical variance (Burnham and Anderson, 1998). Program RELEASE revealed some overdispersion in the data and QAICc (Akaike Information Criterion corrected for small sample size and overdispersion) was used to account for this extra binomial variation (Burnham and Anderson, 2002). The expected number of recaptures was greater than observed
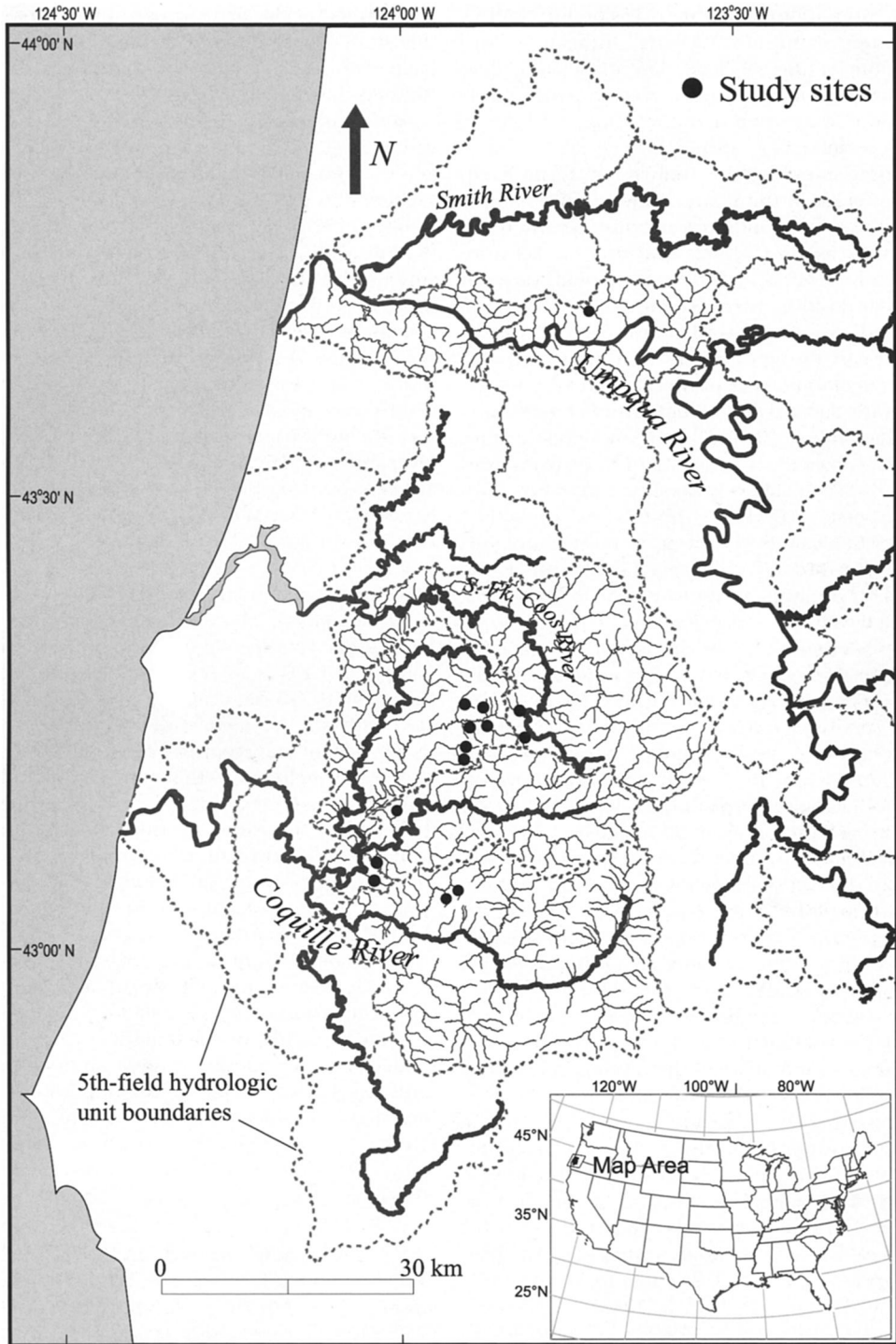
Fig. 1.   Map of southwestern Oregon showing the location of study area and the 14 study sites within the Coquille, Coos, and Umpqua River basins.

for the non-summer capture occasion but not for the other capture occasions, indicating low detection in June of 2003. Overdispersion, due in part to one capture occasion with poor detection, was accounted for using a variance inflation factor ($\hat{c} = 1.6$).

Before beginning the analysis, we formulated an a priori list of candidate models that reflected hypotheses concerning the effects of stream type, age, and season on salamander survival. We also hypothesized that capture-rates would vary by age, year, and the presence of a culvert. We first modeled capture rates (Lebreton et al., 1992), varying survival by time only and then used the most parsimonious capture-rate model to proceed with survival modeling (number of candidate models = 20). We used model selection methods based on the Akaike Information Criterion corrected for small sample size and overdispersion (QAICc), with the ratio of Akaike weights to evaluate the strength of evidence for competing models and specific effects. Time effects on survival and capture probabilities were modeled in two ways: standard CJS time dependent models (time) in which all capture occasions and survival intervals were separately estimated; and seasonal models (season) in which survival intervals were grouped according to season (one-month summer intervals coded separately from the ten-month non-summer interval). Capture probabilities were not modeled by season because all capture occasions occurred in the summer. In the same analysis, we compared larval D. tenebrosus survival and capture probabilities between culvert and reference streams. Competing models were considered those within 4 QAICc units (Δ QAICc $\leq$ 4) of the top model. We used the ratio of Akaike weights (evidence ratio) to determine how well a model was supported by the data. We included an evidence ratio of ≥ 8 as the minimum level for "strong" evidence of an effect (Royall, 1997).

We assigned larval salamanders to age classes at first capture. Age classes were based on earlier studies and the mean size of second-year recaptures in this study. The exact size at which first-year larvae become second-year larvae varies by region and study. Previous studies suggest first-year larvae range in SVL from 35 to 51 mm (36–61 mm, Kessel and Kessel, 1943; 35–57 mm, Nussbaum and Clothier, 1973). We used these estimates to assign first-year larvae to preliminary groups in this study, and then used the size of those individuals recaptured after a year to determine the transition between first- and second-year age classes. Salamanders that appear in streams after hatching are presumed to be first-year larvae, and our lower size limit was

determined by the smallest size of salamanders in this study. We combined second- and third-year larvae because it was difficult to distinguish these two age classes using size data.

Salamander age class was treated as a group variable because animals remained in their initial age class for more than one interval. Most larval salamanders grew into the next age class over the non-summer period ($n = 2,154$). Larval salamanders that grew into the next age class over the summer ($n = 30$), however, may differ from those occupying a distinct age class. We ran the age analysis with and without these individuals to see if their inclusion changed results. The number of these individuals was low and model results were not altered, so we included them in the analysis, using their size at first capture. Overwintering larvae were assigned a subsequent age class in the last two capture occasions and the last survival interval. We set up age-structured PIMs in program MARK to account for this "aging" effect.

We selected a small set of a priori models to describe general characteristics associated with salamander growth. We used a regression model (PROC MIXED; SAS Institute 1999, SAS/STAT Users Guide) to determine if growth was associated with size of salamander at initial capture (SVL), age, or culvert presence. A null model (no effect) was included in the analysis to determine if the response mean was a better fit to the data than any of the other measures. To determine annual growth in relation to size of salamander, we used growth of salamanders captured in June 2002 and recaptured in June 2003. We then ranked models for salamander growth using Akaike's Information Criteria (AICc, adjusted for small sample size). We examined both linear and quadratic relationships between age and growth of salamanders. Competing models were considered those within four QAICc units (Δ QAICc $\leq$ 4) of the top model. We included individual stream ($n = 14$) as a random effect.

RESULTS

We individually marked 2,215 D. tenebrosus (1,334 in June 2002; 881 in July 2002) across 14 stream sites. Of those larvae marked, 1,200 (54%) were recaptured at least once during the study. First-year larvae transitioned into second-year larvae at approximately 54 mm SVL ($\bar{x} = 54$ mm, SE = 0.04, $n = 49$). First-year salamanders in this study were 29 to 53 mm ($n = 1651$), second- and third-year salamanders were 54 to 99 mm ($n = 533$), and aquatic adults ($n = 31$) were >100 mm. Low frequency of aquatic adult

TABLE 1. MODEL SELECTION RESULTS BASED ON QAICc FOR THE NINE TOP MODELS (AND NULL MODEL) OF SURVIVAL (Φ) AND RECAPTURE (p) OF LARVAL *Dicamptodon tenebrosus* USING THE CORMACK-JOLLY-SEBER APPROACH IN PROGRAM MARK (WHITE AND BURNHAM, 1999). This study was conducted on 14 streams in the Oregon Coast Range during the summers of 2002 and 2003. Model variables include age of larval salamander (first-year or second/third-year), season (summer or non-summer), the presence of a culvert on the study stream, and time (between four capture occasions). Interactions between variables are symbolized by a "*" and additive effects are symbolized by a "+". *Minimum QAICc value = 4220.295

Model number	Variables	Likelihood	Number of parameters	Δ QAICc	Akaike weights	Evidence ratio
1	Φ (age+season) p (age*time)	1.000	11	0	0.324	1.000
2	Φ (age+culvert+season) p (age*time)	0.695	12	0.729	0.225	1.440
3	Φ (age*season) p (age*time)	0.528	12	1.278	0.171	1.895
4	Φ (age*time) p (age*time)	0.306	14	2.37	0.099	3.271
5	Φ (age+time) p (age*time)	0.227	13	2.97	0.073	4.415
6	Φ (age+culvert+time) p (age*time)	0.175	14	3.491	0.057	5.729
7	Φ (age+season) p (age+time)	0.107	8	4.468	0.035	9.337
8	Φ (age+season) p (age+culvert*time)	0.034	18	6.743	0.011	29.122
9	Φ (age) p (age*time)	0.013	10	8.737	0.004	78.925
10	Φ (.) p (.)	0.000	2	53.402	0.000	3.945E+11

recaptures (5 recaptures/31 marked), however, precluded their inclusion in the analysis.

The best approximating models suggested an additive age and seasonal/time effect on apparent survival and an interactive age and time effect on capture probability (Table 1). The seasonal model showed a somewhat greater effect than the time dependent model for predicting apparent survival, although there was not strong evidence for a difference (Model 1 vs. 5, evidence ratio = 4.4; Table 1). The 95% confidence intervals on the regression coefficients overlapped zero (β = 0.09, 95% CI = −0.03 and 0.21); hence, model selection results for a culvert effect were inconclusive. All six competing models had both a seasonal/time and an age effect on apparent survival (Table 1).

Using model-averaged estimates, first-year salamander larvae had lower apparent survival estimates than second/third-year larvae over the annual cycle, with no overlapping confidence intervals (effect size = −0.10; confidence interval = −0.05, −0.16; Table 2). Monthly non-summer apparent survival was higher than monthly summer apparent survival for both age classes. However, with biologically important and unimportant values, the result of the difference in season was inconclusive for second/third-year salamanders (first-year effect size = 0.09; confidence interval = 0.05, 0.13; second/third-year effect size = 0.06; confidence interval = 0.03, 0.09; Table 2). Given that most of the covariances were near zero, we estimated standard errors of annual apparent survival using Goodman's For-

TABLE 2. MODEL-AVERAGED ESTIMATES AND CONFIDENCE INTERVALS (CI) OF APPARENT SURVIVAL AND RECAPTURE RATES OF LARVAL *Dicamptodon tenebrosus* USING THE CORMACK-JOLLY-SEBER APPROACH IN PROGRAM MARK (WHITE AND BURNHAM, 1999). Model variables include age (first-years, second/third-years) and season (summer, non-summer) on 14 streams in the Oregon Coast Range between 2002 and 2003. Summer season was between June and August 2002, and non-summer was between August 2002 and June 2003. Recapture estimates and confidence intervals are given for the four capture occasions (1st–4th) between June 2002 and June 2003.

	Age	
Estimates	1st year	2nd/3rd year
Survival		
Summer	0.76 (0.72–0.79)	0.84 (0.80–0.87)
Non-summer	0.85 (0.84–0.87)	0.90 (0.88–0.91)
Recapture occasion		
1st	0.60 (0.55–0.64)	0.41 (0.35–0.48)
2nd	0.64 (0.59–0.68)	0.46 (0.41–0.53)
3rd	0.39 (0.30–0.48)	0.47 (0.37–0.59)
4th	0.73 (0.56–0.85)	0.58 (0.43–0.71)

TABLE 3.   MODEL SELECTION RESULTS BASED ON AICc FOR THE SIX MODELS (AND NULL MODEL) FOR GROWTH OF LARVAL *Dicamptodon tenebrosus*. This study was conducted on 14 streams in the Oregon Coast Range during the summers of 2002 and 2003. Model variables include size of larval salamander (snout vent length, SIZE), presence of a culvert on the study stream (CULVERT), and age (1st or 2nd/3rd year old, AGE). Interactions between variables are symbolized by an "*". Minimum AICc value = −190.73

Model number	Variables	Δ AICc	Likelihood	Akaike weight	Evidence ratio
1	SIZE	0	1.000	0.673	1
2	SIZE * CULVERT	2	0.353	0.238	2.83
3	SIZE * SIZE	4	0.133	0.090	7.50
4	AGE * AGE	98	0.000	2.967E−22	2.27E+21
5	AGE	98	0.000	2.967E−22	2.27E+21
6	Null model	159	0.000	2.112E−35	3.19E+34
7	CULVERT	161	0.000	7.409E−36	9.08E+34

mula (Goodman, 1960), assuming independence between variables. Annual apparent survival for first-year larvae was therefore 0.13 (SE = 0.03) and 0.28 (SE = 0.08) for second/third-year larvae.

In all competing models for capture probabilities, the relationship between age class and time was interactive, rather than additive (Model 7 vs. 1, evidence ratio = 9.3; Table 1). Monthly capture probabilities from model averaging were generally higher for first-year larvae than second/third-year larvae, and the third and fourth capture periods were inconclusive (Table 2).

The top competing models indicated annual growth rates varied by size with smaller salamanders growing faster than larger salamanders (Model 4 vs. 1, evidence ratio = 2.27+21; Table 3). There was some evidence of a slightly quadratic relationship over the annual cycle (Model 3 vs. 1, evidence ratio = 7.50; Table 3). We did not detect a difference in growth rates between reference and culvert streams (Model 7 vs. 1, evidence ratio = 9.08E + 34; Table 3). Metamorphosis occurred between the sizes 53

Fig 2.   Snout–vent length of larval *D. tenebrosus* at onset of metamorphosis from 14 study streams in the Oregon Coast Range.

and 81 mm with 23% occurring after the first year and 77% occurring after the second and third year (Fig. 2).

DISCUSSION

High selection pressure early in the larval period affects survival to metamorphosis. Like many amphibian species that produce numerous young, apparent survival for first-year *D. tenebrosus* larvae was lower than for subsequent age classes (Wilbur, 1980). The >5% difference in the effect of age on survival is potentially biologically significant. Nussbaum and Clothier (1973) estimated first-year survival to be 43%, based on the ratio of first- to second-year larvae in the population. Similarly, research in British Columbia indicated a 30–35% annual mean survival rate for all larval ages (Ferguson, 1998). Our apparent annual survival estimates for first-year larvae were much lower (first-year: 13%; second/third-year: 28%), perhaps due to differences in methodology, demography, or environmental conditions. This study, however, is the first to reliably estimate larval salamander survival based on capture-recapture methods.

Larval survival during the second/third year is likely higher than reported in this study, given that mortality and metamorphosis, which we did not quantify, are confounded for apparent survival estimates under the CJS model, potentially resulting in an even larger difference in apparent survival rates between the two age classes. First-year larval *D. tenebrosus* are prey for juvenile salmonids but may grow large enough by their second year to attain a size refuge from gape-limited predators (Parker, 1993). In addition, second- and third-year larvae are able to exploit larger prey items (Parker, 1994), thereby increasing their access to potential food resources. More than twice as many larval salamanders metamorphosed after the second year than
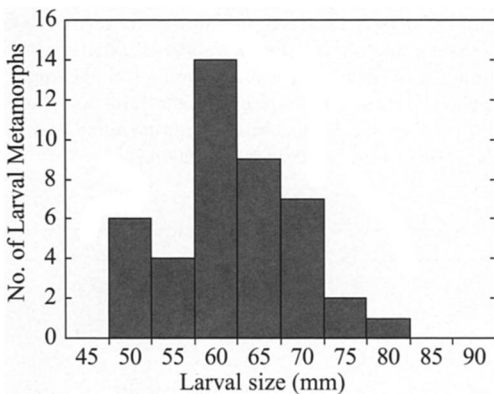
after the first year (Fig. 2), indicating that the aquatic environment may provide continued benefits for larvae that survive their first year.

Growth rates were highest for first-year larvae (Fig. 2) but are also the most variable compared to older age classes. The variability in growth rates may result from variation in stream conditions. Laboratory and field studies have demonstrated that larval salamander growth can be influenced by environmental factors such as temperature and food resources (Petranka, 1984), larval density (Wilbur, 1980; Scott, 1990; Buskirk and Smith, 1991), and presence of predators (Figiel and Semlitsch, 1990; Beachy, 1997).

Differential growth rates during the larval period may affect the life history path (aquatic or terrestrial) of an individual. Rapid growth rates may delay metamorphosis in order to capitalize on favorable stream conditions and the reverse may be true for slow growth rates (Werner, 1986). Coriell (2003) set up a feeding experiment with two populations of second-year larval *D. tenebrosus* from medium-sized streams and found that the group that was fed less had significantly higher rates of metamorphosis. In addition, larvae from small and large streams had different rates of metamorphosis when held under the same conditions, indicating that life history path may be determined before the second year.

The capture probabilities for larval *D. tenebrosus* were relatively high (mean for first-year 59%, second/third-year 48%), given that salamanders were hand captured in moving water. These are some of the first data to quantify capture probabilities for larval stream salamanders, so comparisons to other stream habitats are not possible. Bailey et al. (2004) estimated terrestrial salamander capture probabilities between 0.20 (SE = 0.04) and 0.35 (SE = 0.03) due to less time spent on the surface. Capture probabilities in this study may indicate low temporary emigration and time mostly spent above ground in the stream channel. Despite their smaller size, first-year salamanders had a higher capture probability than second- and third-year salamanders throughout the summer. Older age classes may be better able to secure refugia and therefore evade detection.

The availability of in-stream habitat takes on critical importance for larval *D. tenebrosus* given the relatively long larval period. Although seasonal demographic rates can be estimated for these populations, a long-term study may be needed to address variation in survival and growth between years. While we found little support for an effect of culverts on growth and survival, effects on larval movement are apparent (Sagar, 2004), suggesting further investigation of the potential effect of culverts on survival may be warranted. In addition, further study is needed to determine growth in terrestrial adults after metamorphosis, although we were able to determine low growth rates for a small sample of paedomorphic adults (Sagar, 2004). Species with little post-metamorphic growth may exhibit a greater correlation between larval quality and adult fitness (Semlitsch, 1987). Maintenance of high quality larval habitat may be critical for providing conditions that foster early growth and survival.

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(JPS, RAS) DEPARTMENT OF FISHERIES AND WILDLIFE, 104 NASH HALL, OREGON STATE UNIVERSITY, CORVALLIS, OREGON 97331; AND (DHO) USDA FOREST SERVICE PACIFIC NORTHWEST RESEARCH STATION, 3200 SOUTHWEST JEFFERSON WAY, CORVALLIS, OREGON 97331. E-mail: (JPS) jpsagar@hotmail.com. Send reprint requests to JP. Submitted: 17 Sept. 2004. Accepted: 28 Aug. 2006. Section editor: S. J. Beaupre.