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## Life History of Postmetamorphic Coastal Tailed Frogs (*Ascaphus truei*) in Northwestern California

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**ABSTRACT.**—We conducted nocturnal surveys of postmetamorphic *Ascaphus truei* on six streams in north coastal California from 2002–04, using mark-recapture techniques to determine sizes of age classes, growth rates, site fidelity, reproductive chronology, and seasonal activity within the stream channel and riparian zone. *Ascaphus truei* grew year-round, but grew faster during the summer ( $1.47 \pm 0.06$  mm/month) than winter ( $0.89 \pm 0.04$  mm/month). Growth curves indicate that following metamorphosis, females likely reached sexual maturity in three years, whereas males became reproductive in two years. Tailed frogs in these coastal streams exhibited limited within-channel longitudinal movement ( $\bar{x} = 13.6$  m), although movements were highly variable (range = 0–112 m). Significantly more frogs were captured in summer than fall, and very few frogs were captured in winter. Significantly more reproductive adults were captured in spring than summer, suggesting that breeding occurred primarily in spring. Recapture data indicated that females deposited eggs in the stream mostly during July and August and may have a biennial reproductive cycle. This study has quantified life history traits for *A. truei* populations in coastal northwestern California that contrast to results for inland and northern *Ascaphus* populations. Comparative geographic variation studies throughout the range of *Ascaphus* are needed to aid in understanding life-history and ecological differences both within and among regions.

*Ascaphus truei* is highly specialized for life in cold, fast flowing, clear, mountain streams (Nussbaum et al., 1983). This species is sensitive to stream habitat alterations, often associated with land management activities such as timber harvest, which result in elevated fine sediment loads and increased water temperatures (Noble and Putnam, 1931; Metter, 1964; Dupuis and Steventon, 1999; Wahbe and Bunnell, 2003). Some studies suggest that such increases in sediment or temperature could result in extirpation of a population from a stream (Metter, 1964; Nussbaum et al., 1983; Corn and Bury, 1989; Welsh, 1990).

Most research on *A. truei* has focused on their distribution (Bury, 1968), habitat (Diller and Wallace, 1999), life history (Noble and Putnam, 1931; Brown, 1990; Wallace and Diller, 1998; Bury and Adams, 1999), or the effects of timber harvest upon this species (Bury, 1983; Corn and Bury, 1989; Welsh, 1990; E. L. Bull and B. E. Carter, U.S. Department of Agriculture, Forest Service, Research Paper, PNW-RP-497, Portland, Oregon, 1996). Such studies have typically involved sampling larvae because of their ease of study relative to adults (but see Welsh and Lind, 2002). Larvae are often abundant in

streams and easy to locate and capture, whereas adults are nocturnal (Metter, 1964) and can be more difficult to sample (Wallace and Diller, 1998). Larvae may also be more susceptible to the effects of timber harvest because they are restricted to streams (Diller and Wallace, 1999).

Concentrating studies on larval populations limits our understanding of the ecology of this species and its sensitivity to land management activities. Critical demographic parameters of postmetamorphic *A. truei* populations are largely unknown or are inferred from the larval populations. For example, within and among stream fluctuations in larval populations have been interpreted as differences in habitat suitability and frog abundance (Corn and Bury, 1989; Welsh, 1990), but breeding cycles of females may also affect these patterns. Quantifying life-history traits of transformed frogs will improve our understanding of the fluctuations and patterns of larval populations.

In Montana, Daugherty and Sheldon (1982b) found that postmetamorphs of *Ascaphus montanus* were active at night from May to September where they were observed sitting out in the open near streams. During the winter, they presumably sought shelter under boulders and logs within the stream. Based on their results for *A. montanus*, these authors postulated that, because of milder climatic conditions, coastal populations of *A. truei* may be active and continue feeding throughout the year (Daugherty and Sheldon, 1982a). However,

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there has been no attempt to quantify growth patterns of *A. truei*.

Differences in the responses of inland and coastal populations of *Ascaphus* spp. to timber harvest have been attributed to differing climatic conditions between these two environments. For example, Diller and Wallace (1999) proposed that the mild, moist conditions of the redwood (*Sequoia sempervirens*) zone of northwestern California, which produce relatively stable year-round temperatures, may help ameliorate the effects of timber harvest on *A. truei* populations in this region (but see Welsh et al., 2000; Ashton et al., 2006). Additionally, there may be geographic variation in reproductive cycles (Metter, 1967; Sever et al., 2001) and movement patterns both within and among *Ascaphus* because of inland and coastal climatic differences (Wahbe et al., 2004). Mark-recapture studies in eastern Oregon, Montana, and British Columbia have examined movement patterns (Landreth and Ferguson, 1967; Daugherty and Sheldon, 1982b; Wahbe et al., 2004; Matsuda and Richardson, 2005), age class structure, and life history of both *Ascaphus* species (Daugherty and Sheldon, 1982a). However, with the exception of coastal British Columbia, these studies involved inland *Ascaphus* populations. Information is lacking for *A. truei* populations in northwestern California. Examining these patterns for postmetamorphic *A. truei* in northwestern California will further the understanding of the ecology of *A. truei* and aid in making land management decisions regarding this species.

The objectives of this study were to determine (1) adult and immature size classes, (2) growth rates, (3) site fidelity, (4) reproductive chronology, and (5) activity patterns and seasonal age and sex composition of populations of post-metamorphic *A. truei* in six streams located in north coastal California.

#### MATERIALS AND METHODS

**Study area.**—We conducted this study on streams located on Green Diamond (formerly Simpson) Resource Company's managed timberlands in Humboldt County, California (41°N, 124°W). The study area is located within the coastal redwood zone and includes the northern portion of the Mad River drainage in Korbel and parts of the Maple Creek drainage just east of Big Lagoon (Fig. 1). Mean summer and winter air temperatures within the study area are ~ 18°C and 5°C, respectively. Coast redwood is the predominant conifer, and forests are comprised of second- to third-growth timber ranging primarily from 0–80 years in age. Historical unregulated logging activities included

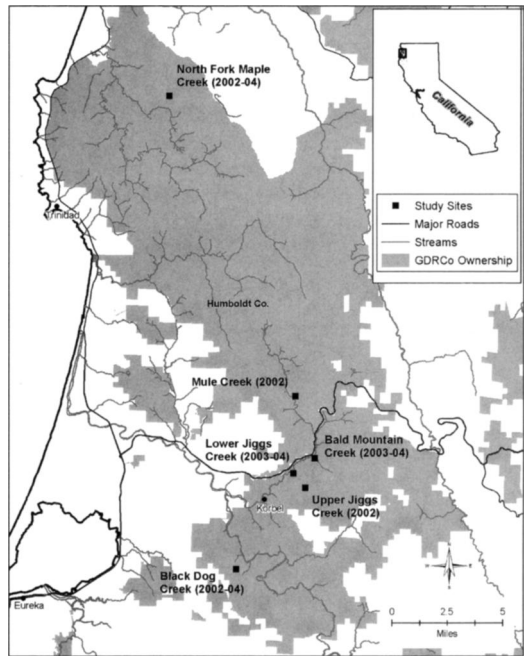


FIG. 1. Locations and survey years for *Ascaphus truei* study streams on Green Diamond Resource Company managed timberlands, Humboldt County, California, 2002–04.

a variety of silvicultural techniques from clear-cutting entire drainages to selective harvest with little to no protection for streams. Since the implementation of the California Forest Practices Act in 1973, protection of streams has increased, and logging practices have shifted to primarily even-aged forest management with small clear-cuts followed by artificial regeneration of stands (see Diller and Wallace, 1999).

As a result of annual amphibian surveys conducted by Green Diamond biologists, several creeks within this area are known to support populations of *A. truei*. We conducted our study in a subset of creeks currently being used to monitor the effects of timber harvest on *A. truei*. Study creeks were tributaries of the Mad River, North Fork Mad River, and Maple Creek (Fig. 1). Creeks varied in size from small second-order channels to a relatively large third-order channel. Drainage areas for study creeks upstream of the survey reaches were Bald Mountain = 12.17 km<sup>2</sup>, Lower Jiggs = 2.69 km<sup>2</sup>, Black Dog = 2.04 km<sup>2</sup>, Upper Jiggs = 1.44 km<sup>2</sup>, Mule = 1.37 km<sup>2</sup>, and North Fork Maple = 1.01 km<sup>2</sup>. These are non-fish-bearing streams with the exception of Mule and Bald Mountain Creeks.

**Study design.**—Green Diamond conducts annual larval *A. truei* surveys on 17 streams throughout the company's land holdings. With-

in logistical constraints of road access, selection of the 17 streams was based on a stratified random approach designed to capture variation in geology, forest type, and amount of recent timber harvest. The primary emphasis was to pair streams with little or no recent harvest with those scheduled for high levels of harvest. We randomly selected four of the 17 streams to survey for adult frogs. For selection, study streams had to be within one hour of travel from the company office in Korbel, California, and easily accessible either by road or trail (less than one-half hour hiking time). In the first year, we had comparatively few frog captures in two of the four study streams. Therefore, for the following two years of the study, the streams with low captures were substituted with two new streams known by company biologists to support large numbers of *A. truei* (L. Diller, unpubl. data). This resulted in a total of six study streams, with four streams surveyed each year (Fig. 1).

Night surveys for *A. truei* were conducted on study creeks from 2002–04. To estimate temporal seasonal variation in captures, each creek was surveyed two to four times per month in spring, summer, and fall and once per month as captures declined in winter.

Reaches monitored for larval *A. truei* ranged from 350–450 m in length. Night survey reaches were 175 m long and placed within larval monitoring reaches so that the start of each night sampling reach was at least 100 m upstream from the start of the established larval monitoring reach. This reach placement was intended to account for potential larval movements, thereby increasing the probability that the adult population sampled would be the source of the larval population in the monitoring reach. The two streams substituted in 2003–04 were higher order streams (Bald Mountain and Lower Jiggs Creeks). Therefore, night survey reaches in these larger streams were shorter in length (80 and 140 m) than those surveyed in 2002 to account for differences in stream width and control for the overall area searched within the stream channel.

*Animal sampling.*—Postmetamorphic *A. truei* are active along the stream channel at night (Nussbaum et al., 1983), and peaks in activity have been observed in northwestern California populations at dusk and dawn (Ashton et al., 2006). We conducted area-constrained visual encounter surveys starting within one-half hour of sunset. Surveys were completed in one to two hours. Capture and handling of *A. truei* were conducted under the provisions of a memorandum of understanding (MOU) between Green Diamond and California Department of Fish and Game.

During surveys, two or more observers began searching at the designated start of the reach and slowly walked along the stream systematically searching the banks and streamside for postmetamorphic *A. truei*. To increase the probability of detecting frogs, the reach was searched first upstream, then back downstream. To avoid double counts, frogs were captured and temporarily detained until completion of the survey. Frogs were located visually, primarily through detection of eyeshine, using a Nite Lite® halogen light to illuminate the search area (Heyer et al., 1994). Frog eyeshine was not easily detected unless the light source was positioned near the observer's eye to gaze directly down the light beam. During the search, the light was cast from the stream edge out to the maximum distance that frogs could be detected. Differences in vegetative cover among survey reaches likely influenced capture probabilities, but searches remained consistent within a given reach to minimize within reach fluctuations in capture probabilities. Surveys were not conducted on nights with heavy rain because of our inability to detect eyeshine in these conditions.

Capture locations for individual frogs were flagged, and each frog was placed in a plastic bag filled with creek water. At completion of the survey, frogs were anesthetized by immersion in a 1.2 g/l buffered solution of tricaine methane sulfonate (MS-222) and given an individual mark by injecting visible implant elastomer (Northwest Marine Technology®) subcutaneously in the fore- and/or hind feet based on a prescribed marking code.

Snout-vent length (SVL) was measured to the nearest 0.1 mm. Frogs were weighed to the nearest 0.1 g. Age and sex (when possible) and reproductive condition (gravid females and males with nuptial pads were considered reproductive) were recorded for each frog. All measurements were done on anesthetized frogs. Male frogs less than 31 mm SVL do not have discernible cloacal extension, and the sex of all individuals in this size class was recorded as unknown. Frogs recaptured within a month were not anesthetized and remeasured, because it was assumed there was too little growth to justify the additional stress to the animal. Newly metamorphosed frogs were categorized as recent metamorphs and given a cohort mark (single mark on the venter). After we had marked frogs, we released them at their point of capture on the same evening.

*Stream measurements.*—To examine upstream and downstream movements of marked frogs, longitudinal distance from the start of the sampling reach to the point of capture was measured to the nearest 0.1 m. Lateral distance was also measured from the place of capture to

both the wetted and active channel (nearest centimeter).

*Data analysis.*—Snout-vent length frequency histograms from May to August were used in conjunction with reproductive data to estimate size and age classes of frogs. The smallest SVL of reproductive male and female frogs (those exhibiting secondary sexual characteristics during the breeding season) were used to determine minimum SVL for the adult (reproductive) age class. Frogs with an SVL less than this minimum value were considered immature (prereproductive). Comparisons were made between male and female SVL using the Wilcoxon rank-sum test corrected for ties. Sample sizes of each age class were insufficient to test for a stream effect. To ensure SVL measurements were independent, only SVL data from the first capture were used for frogs recaptured within the same year.

Growth was examined using the von Bertalanffy growth model (Bertalanffy, 1938). This is an asymptotic model commonly used for a variety of animals including fish and amphibians, under the assumption that growth decreases linearly with body size (Shine and Charnov, 1992; Lima et al., 2000; Diller and Wallace, 2002). Growth data were fit for males and females separately to the following growth equation:  $SVL_t = SVL_{\max}[1 - e^{-k(t - t_0)}]$ , where  $SVL_{\max}$  was maximum SVL,  $k$  was the growth coefficient,  $t$  was the number of days since first capture, and  $t_0$  was a hypothetical negative number representing the number of days when the SVL of the animal would be zero. Only frogs that were first captured as juveniles and then subsequently recaptured were entered into the growth model. We estimated juvenile size of frogs within streams using recapture data of frogs first marked as recent metamorphs and recaptured the following spring or summer (juvenile males: mean SVL =  $32.8 \pm 0.58$  mm,  $N = 5$ ; juvenile females: mean SVL =  $34.8 \pm 0.54$  mm,  $N = 6$ ). Mean SVLs, truncated to the nearest integer, were used to assign minimum lengths for juvenile males and females. Growth rates,  $k$ , between males and females were compared using a two-sample  $z$ -test. Streams were pooled because of small sample sizes.

The von Bertalanffy growth equation and estimated parameters were used to estimate time to sexual maturity for males and females separately. The SVLs of the smallest reproductive frogs were used in the growth equation to estimate  $t$ , the number of days from juvenile age to reach that reproductive size (SVL).

We examined site fidelity between frogs of different age and sex classes using the Kolmogorov-Smirnov test (Sheskin, 2000) to compare longitudinal distances moved. This test was

used because transformations of the data did not meet the assumptions of normality and equal variance.

Because of logistical and safety considerations of accessing streams at night, streams were consistently searched from the same starting location. Given the potential bias in observations of frog movements, we used the absolute value of longitudinal distances moved within the stream channel relative to the first capture location as the dependent variable. Because there were no significant differences between longitudinal movements for frogs captured in multiple years compared to frogs recaptured within a year (Kolmogorov-Smirnov test, adult females:  $P = 0.52$ ; adult males:  $P = 0.09$ ; immature females:  $P = 0.40$ ; immature males:  $P = 0.33$ ), we pooled streams and included all frogs that were recaptured at least three times in the analysis. All movements of individual frogs were considered independent because distances moved from one capture to the next were measured with at least one to two weeks between surveys, and in most cases, there were several months between captures.

We compared the number of reproductive adults between sexes, years, and streams using an analysis of variance (ANOVA). Because the number of surveys among seasons was not equal, we used the number of frog captures divided by the number of surveys per season as the dependent variable. The number of reproductive adults was compared between seasons (spring and summer) using a two-sample  $t$ -test. Reproductive adult captures were further explored using ANOVA to compare annual variation in the number of reproductive males and females captured in spring. If results were significant, multiple comparisons were made using the Tukey-Kramer test.

Activity patterns of frogs in different age and sex classes were compared using log-linear models. This analysis is an extension of the chi-square test, which allows for exploration of multiway relationships among variables, while requiring few assumptions about population distributions (Afifi and Clark, 1996). We examined all main effects and two-way interactions of the factors year, stream, age, sex, and season. Because of a significant stream effect, we only examined results from this analysis for 2003 and 2004 when the same streams were surveyed each year.

Recent metamorphs and frogs recorded as unknown sex were excluded from the analyses. All tests were evaluated at an alpha level of 0.05. For all ANOVA analyses, natural log- or square-root transformations of the data were used when necessary to meet assumptions of

normality of residuals and equal variance among groups. Means are given as  $\pm 1$  SE.

### RESULTS

Between 2002 and 2004, we conducted 211 surveys and captured 2,146 postmetamorphic *A. truei*. The total number of recaptures was 1,397 with 37.8% of all frogs recaptured more than once. Yearly capture totals of individual frogs were 351, 980, and 815 for 2002–04, respectively. Mean captures for creeks over all years were Black Dog Creek =  $135 \pm 22$  ( $N = 3$ ), Maple Creek =  $103 \pm 21$  ( $N = 3$ ), Bald Mountain Creek =  $327 \pm 40$  ( $N = 2$ ), Lower Jiggs Creek =  $323 \pm 33$  ( $N = 2$ ), Mule Creek =  $47$  ( $N = 1$ ), and Upper Jiggs Creek =  $84$  ( $N = 1$ ). In 2002 and 2003, 26.5% of all frogs were recaptured one or more times, whereas 29.0% were recaptured in 2004. The percentage of recaptures averaged  $27.4 \pm 2.5\%$  over all creeks and years.

**Size classes.**—The SVLs of the smallest reproductive frogs were 34 and 42 mm for males and females, respectively. These lengths were used as cut-off values to separate frogs into adult (reproductive) and immature (prereproductive) age classes. The SVL distributions of reproductive frogs (Fig. 2) further supported these cut-off values. Because of overlap in the SVL frequency distributions, we were not able to delineate between additional age classes for frogs within the prereproductive category (Fig. 2). Females were significantly larger than males for both age classes (Wilcoxon rank-sum test, adult females: mean =  $44.4 \pm 0.4$  mm,  $N = 218$ , adult males: mean =  $36.7 \pm 0.2$  mm,  $N = 350$ ,  $Z = 20.1$ ,  $P < 0.00001$ ; immature females: mean =  $34.6 \pm 0.4$  mm,  $N = 362$ , immature males: mean =  $32.0 \pm 0.4$  mm,  $N = 212$ ,  $Z = -13.6$ ,  $P < 0.00001$ ).

**Growth.**—Because of the good fit of the data to the von Bertalanffy growth model (Table 1), reliable estimates of growth were obtained for frogs within the study area. Evidence of an asymptotic growth pattern can be seen by comparing growth curves to plots of SVL versus days since first capture for adult frogs (Fig. 3).

Although SVL analyses showed that females were larger than males, growth rates between males and females were not significantly different ( $Z = 1.31$ ,  $P = 0.19$ ). *Ascaphus truei* grew year-round, but mean summer growth was faster (males =  $1.42 \pm 0.09$  mm/month,  $N = 62$ ; females =  $1.50 \pm 0.08$  mm/month,  $N = 81$ ; month = 30 days) compared to winter growth ( $0.89 \pm 0.04$  mm/month,  $N = 7$ ). However, winter sample sizes were insufficient to separate by sex or to permit statistical comparisons between seasons. Growth curves indicated that females likely reached sexual maturity during

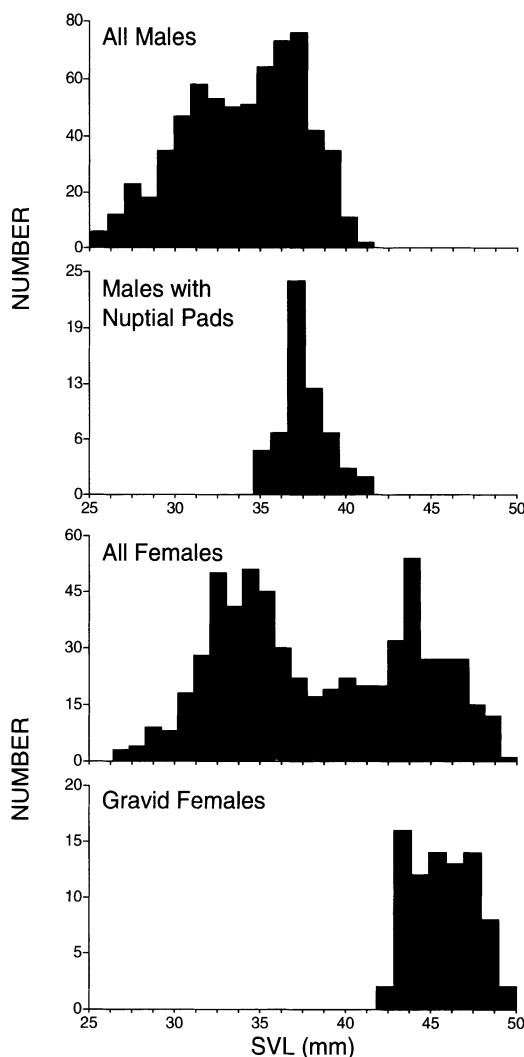


FIG. 2. Snout-vent length distributions from May through August for male and female *Ascaphus truei* for six streams in coastal northwestern California, 2002–04. Data from first capture only were used for frogs recaptured within the same year.

their third spring following metamorphosis at approximately two and a half to three years of age ( $t = 434$  days from juvenile age). Transformed males likely became reproductive during their second spring at approximately one and a half to two years of age ( $t = 170$  days from juvenile age; Fig. 3).

**Site fidelity.**—Immature and adult frogs appeared to exhibit fidelity to an area within the stream channel. Both mean upstream and downstream movements were minimal. Distributions of longitudinal movements relative to the axis of the stream showed that most frogs moved from 0–30 m within the stream channel (Fig. 4). The distribution of longitudinal movements for adult females differed significantly

TABLE 1. Von Bertalanffy growth model results for *Ascaphus truei* first captured as juveniles in coastal northwestern California, 2002–04.

Parameter	Parameter estimate	Lower 95% CI	Upper 95% CI	$r^2$
<i>Males</i>				
Maximum SVL (mm)	39.49	36.72	42.26	0.65
Growth coefficient (k)	0.0035	0.0018	0.0052	
$t_0$	-386.36	-520.50	-252.21	
<i>Females</i>				
Maximum SVL (mm)	49.50	42.20	56.79	0.74
Growth coefficient (k)	0.0021	0.00091	0.0033	
$t_0$	-447.34	-600.23	-294.44	

from that of adult and immature males (Kolmogorov-Smirnov test:  $D_{max} = 0.23, P = 0.01, N_1 = 62, N_2 = 197, D_{max} = 0.27, P = 0.003, N_1 = 62, N_2 = 129$ , respectively), indicating that adult females made larger longitudinal movements relative to males (Fig. 4). There was no significant difference in the distribution of longitudi-

nal movements between immature males and females ( $D_{max} = 0.08, P = 0.70, N_1 = 129, N_2 = 126$ ). Adult females, however, moved significantly farther than immature females ( $D_{max} = 0.29, P = 0.001, N_1 = 62, N_2 = 126$ ; Fig. 4). There was no significant difference in longitudinal movement distributions for males in different age classes ( $D_{max} = 0.11, P = 0.25, N_1 = 197, N_2 = 129$ ). Over all years, the mean percentage of total frogs captured within 5 m of the water was 94.9%, whereas 4.7% and 0.4% were found within 5–10 m, and > 10 m, respectively. We captured 59.8% of frogs outside and 40.2% within the active channel. For those frogs not captured within the active channel, 24.6% were found on the margin of the active channel, 73.5% were < 5 m, and 1.9% were from 5–10 m from its margin.

*Reproductive chronology.*—Breeding appeared to occur primarily in spring with significantly more reproductive adults captured in spring ( $1.47 \pm 0.16$  frogs per survey periods) than summer ( $0.22 \pm 0.04$  frogs per survey periods,  $t = 7.42, P < 0.00001$ ). There were no significant differences in number of reproductive adults captured during spring or summer with respect to sex (spring:  $F = 0.00, df = 1,22, P = 0.98$ ;

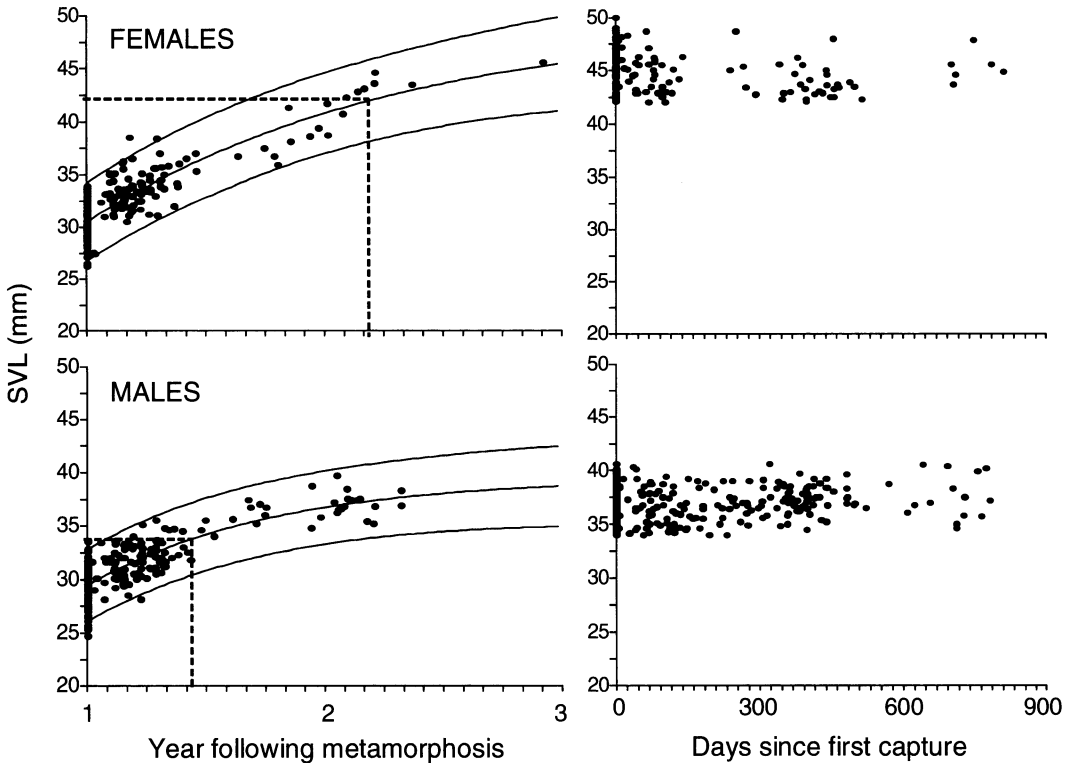


FIG. 3. Growth plots for male and female *Ascaphus truei* in coastal northwestern California, 2002–04. Plots on the left show von Bertalanffy growth curves for frogs first captured as juveniles. Dashed lines represent minimum SVLs for reproductive frogs and estimates of time to sexual maturity. Plots on the right show recaptures of frogs first captured as adults.

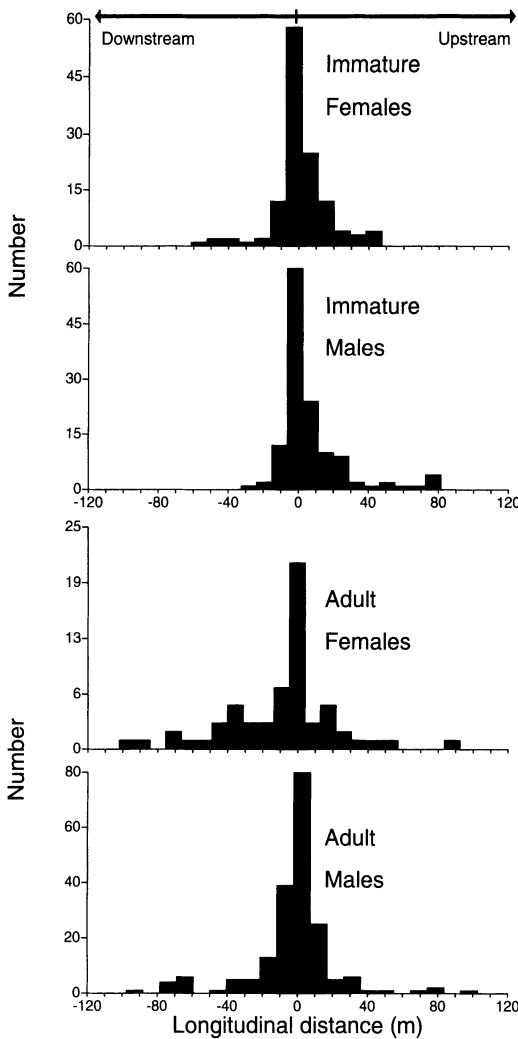


FIG. 4. Distributions of longitudinal movements relative to the first capture location for *Ascaphus truei* in coastal northwestern California, 2002–04. Only frogs with three or more captures were included.

summer:  $F = 0.02$ ,  $df = 1,22$ ,  $P = 0.90$ ), year (spring:  $F = 2.26$ ,  $df = 2,21$ ,  $P = 0.13$ ; summer:  $F = 0.44$ ,  $df = 2,21$ ,  $P = 0.65$ ), or stream (spring:  $F = 0.99$ ,  $df = 5,18$ ,  $P = 0.45$ ; summer:  $F = 2.66$ ,  $df = 5,18$ ,  $P = 0.06$ ). When comparing captures in spring only, significantly more reproductive females were captured in 2002 than in 2003 and 2004 ( $F = 12.41$ ,  $df = 2,9$ ,  $P = 0.0026$ ). There was no significant annual variation in captures of reproductive males ( $F = 0.54$ ,  $df = 2,9$ ,  $P = 0.60$ ; Fig. 5). Recapture data indicated that oviposition occurred mostly during July and August, and possibly as late as September, for all years (Fig. 6).

*Variation in captures.*—Frogs were captured within the stream channel and riparian zone from March to November with peak captures

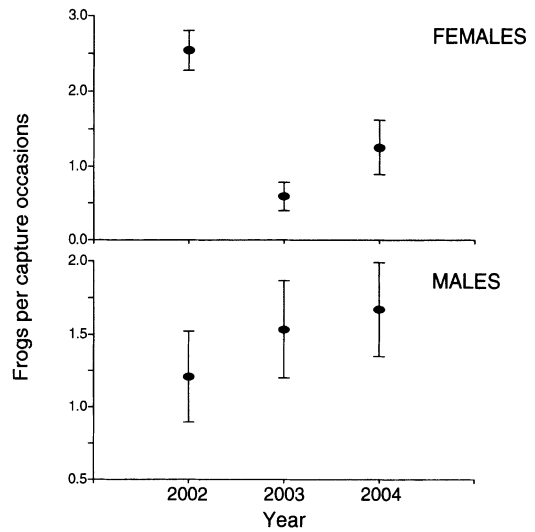


FIG. 5. Annual variation in mean  $\pm$  SE spring captures of reproductive adult male and female *Ascaphus truei* in coastal northwestern California, 2002–04.

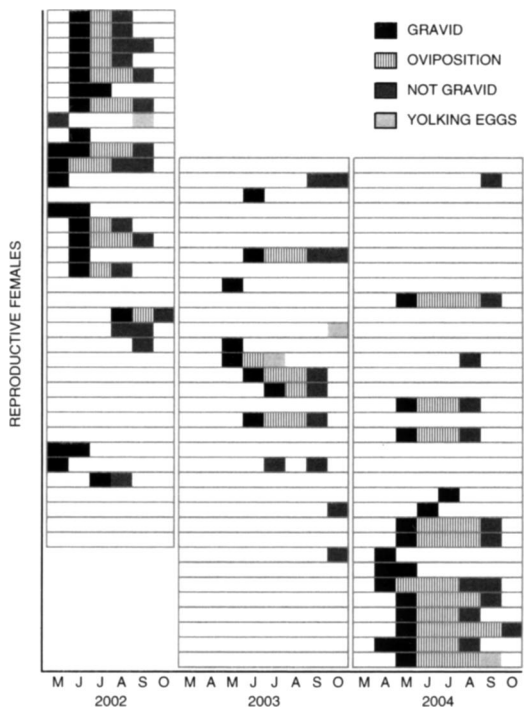


FIG. 6. Frequency of reproduction and timing of oviposition for female *Ascaphus truei* from six streams in coastal northwestern California, 2002–04. Horizontal bars represent individual adult females. Includes all captures of gravid females over the study period.



from July to September for adults and from May to August for immature frogs. The best model generated by the log-linear analysis included the variables stream, age, sex, season, and the interaction between age and sex and had good fit to the data ( $\chi^2 = 82.46$ ,  $df = 87$ ,  $P = 0.62$ ). According to the model, there were significantly more captures in Bald Mountain Creek (36.9%) and Lower Jiggs Creek (34.0%), followed by North Fork Maple (15.4%) and Black Dog (13.8%) Creeks. Significantly more adult males (72.0%) were captured than females (28.0%), whereas captures of immature frogs were similar for males (47.9%) and females (52.1%). Seasonal captures varied with significantly more frogs captured in summer (45.6%) than fall (24.0%), but neither was significantly different than spring (30.4%). Overall, captures were highest in summer, followed by spring and fall with the fewest in winter (only two to three frogs per capture period). Sample sizes were too small to include winter captures in the analysis.

#### DISCUSSION

*Size classes and growth.*—Length frequency histograms seemed to provide reliable cut-off values between reproductive and immature frogs. However, we were unable to make a distinction based on size among other age classes of frogs, which may have been caused by continuous growth throughout the year in coastal populations as predicted by Daugherty and Sheldon (1982a). We were able to estimate juvenile size from recapture data, which allowed us to estimate juvenile age for subsequent growth analyses.

There is likely geographic variation in size and age classes among *Ascaphus* spp. (Daugherty and Sheldon, 1982a). Several researchers have proposed that growth rates may vary with elevation and latitude between inland and coastal *Ascaphus* populations (Metter, 1967; Daugherty and Sheldon, 1982a; Brown, 1990; Wallace and Diller, 1998). Because of the shorter growing season at high elevations (Metter, 1967; Brown, 1990), *Ascaphus* tadpoles may take three to four years to complete metamorphosis (Metter, 1967; Brown, 1990; Bull and Carter, 1996) compared to one to two years for coastal *A. truei* populations (Adams and Bury, 1994; Wallace and Diller, 1998; Bury and Adams, 1999). There is likely similar geographic variation in growth patterns for postmetamorphic frogs (Metter, 1967; Daugherty and Sheldon, 1982a). As a result, the size classes we identified may only be appropriate for coastal populations of *A. truei* within our study area.

Daugherty and Sheldon (1982a) speculated that *A. truei* inhabiting coastal areas may grow more rapidly and mature at a younger age than *A. montanus*. Our study is the first attempt to estimate time to sexual maturity for *A. truei* using growth curves. *Ascaphus truei* in our study area reached sexual maturity faster than has been reported for *A. montanus*. Males and females require approximately two and three years, respectively, to reach sexual maturity following metamorphosis in contrast to three and four years to maturity for *A. montanus* (Daugherty and Sheldon, 1982a). Difference in time to sexual maturity is especially pronounced when including the larval period, which was one year within our study area (Wallace and Diller, 1998) compared to three to four years for *A. montanus*.

*Site fidelity and movement.*—Adult *Ascaphus* have been reported to exhibit site fidelity within the stream channel, whereas juveniles were found to be the main dispersers (Daugherty and Sheldon, 1982b; Wahbe et al., 2004; Matsuda and Richardson, 2005). Both immature and adult frogs appeared to exhibit site fidelity in our study area. Because most upstream and downstream movements were less than 30 m within stream reaches, it is likely that direction of movement was not important. However, there was the potential for frogs to move large distances within or away from the stream channel during intervals when they were not recaptured. Therefore, our estimates of movement are conservative, reflecting only that individuals returned to a general area within the stream channel over multiple years. Although we captured most frogs within 5 m of the water and active channel, this is likely biased by a greater probability of detecting frogs closer to the stream in the relatively open channel compared to the densely vegetated riparian zone.

Landreth and Ferguson (1967) and Brown (1975) have reported large local movements during the breeding season for females. Wahbe et al. (2004) provided evidence for movements from uplands to streams or stream-to-stream breeding migrations by female *A. truei* in coastal British Columbia. They suggested that, because females store sperm and may breed every other year, it was possible that they moved upland from the stream and later returned to deposit eggs. In the Blue Mountains of southeastern Washington, Metter (1964) observed seasonal movements of adult *A. montanus*, with fewer adults found in the late summer than spring. He concluded that frogs may have moved upstream to areas having more shade and vegetation. Adult frogs may also move upstream because intermittent headwaters streams provide more food (Hayes et al., 2004). Adult females in our study area moved farther on

average than immature frogs and adult males. Variation in seasonal captures further suggests differential movements between the sexes and age classes, although our study was not designed to identify movements outside sample stream reaches. However, anecdotal observations by Green Diamond biologists working within the same watersheds indicate that both immature and adult *A. truei* can be found in first-order headwater streams and seeps throughout the year.

*Reproductive chronology.*—Noble and Putnam (1931) suggested annual breeding for *A. truei* females in coastal populations on the Olympic Peninsula in Washington. Metter (1964, 1967) also suggested annual breeding for coastal females. In contrast, inland and northern populations of *Ascaphus* spp. appeared to breed every other year. In our study, annual variation in the number of reproductive females captured suggests that females may not breed every year but may have a biennial reproductive cycle in north coastal California. Only one female was observed to be gravid in two successive years. However, recapture data were insufficient to determine whether that female oviposited in both years or retained her eggs from one season to the next. We typically did not recapture reproductive females during the breeding season (spring) of the year following an apparent breeding attempt, but many were recaptured during the next fall. This annual variation in the number of reproductive females is best explained by a biennial breeding cycle for females, in which nonbreeding adult females moved out of the breeding streams into headwater tributaries or other upslope locations to possibly increase foraging opportunities or reduce predation pressures.

There may be variation in reproductive cycles among individual females within a population, but localized changes within the stream environment could create a situation that promotes synchronization of the breeding cycle in females. For example, localized disturbances within a stream or watershed such as landslides, debris torrents, or drought in a particular year could produce such an effect (e.g., Metter, 1968). Because there was no significant difference in the number of breeding males among years, it is likely that the annual variation in the number of breeding females was caused by cyclical breeding. Annual larval *A. truei* monitoring data collected from 1997 to the present on streams within our study area showed annual cyclic variation in larval abundance for at least some streams (L. Diller, unpubl. data), which is consistent with a biennial breeding pattern for females. However, it will require telemetry methods to further elucidate movement patterns and breeding cycles for females.

Although Metter (1967) suggested that *Ascaphus* breed during the fall throughout their range, our captures of reproductive adults suggest that breeding occurred primarily in spring within our study area. This contrasts to the breeding season reported for inland populations of *A. truei* in the Cascade Mountain ranges and for *A. montanus* populations in Montana and Idaho. Breeding in these high-elevation inland sites has been observed in fall following snowmelt and high flows (Metter, 1964, 1967). In the absence of snow, the maritime climate of coastal areas may allow breeding to occur in spring and summer as stream flow decreases following winter rains.

Temporal variation in breeding seasons probably also exists between coastal and inland populations of *A. truei* in northern California. Although no published studies exist, males with nuptial pads have been observed in the fall at high elevations in the Trinity Alps, located east of Humboldt County, California. One pair was also observed in copulexus in October (J. Garwood, pers. comm.). Another male with a very large swollen cloaca, suggesting recent copulexus, was observed during fall at an inland site in South Fork Mountain, Trinity County, California (L. Diller, pers. obs.).

An extended breeding season at low elevations has been reported for many amphibian species (Morrison and Hero, 2003). However, there may also be latitudinal variation in breeding seasons among coastal populations of *A. truei*. Noble and Putnam (1931) reported a prolonged breeding season for coastal *A. truei* in the Olympic Mountains of Washington where they captured reproductive males and females in late summer and early fall. In our study area, the breeding season appeared to peak in spring, and we observed no reproductive adults during the fall.

Females oviposited during July and August, and possibly September, for all years and streams in our study area. It is likely that females deposited their eggs after mating in the spring and summer of the same year, indicating a one-year reproductive cycle. Sever et al. (2001) examined reproductive histology of *A. truei* collected within the same watersheds as our study and suggested that these frogs begin developing eggs in fall and then deposit those eggs in the stream the following summer after mating. Daugherty and Sheldon (1982a) suggested a two-year reproductive cycle for *A. montanus* in the Rocky Mountains, where females began developing eggs in fall, retained those eggs through the year, mated the next fall, and then further retained those now fully developed eggs for oviposition the following June. This two-year pattern was also documen-

ted by Metter (1967) for inland *Ascaphus* populations in Oregon, Washington, Idaho, and Montana. However, although there seems to be geographic variation in female reproductive cycles, oviposition appears to occur primarily during the summer (Noble and Putnam, 1931; Metter, 1964, 1967; Brown, 1975) when stream flows are low (Daugherty and Sheldon, 1982a; Adams, 1993) for both inland and coastal *Ascaphus* populations.

*Variation in captures.*—Significant variation in captures by age, sex, season, and stream suggests that there was a large amount of variation in the number of frogs found within the channel on any particular survey. Variation in the number of frogs found within the stream channel at night could have been caused by variation in foraging cycles. Frogs may not have required food nightly and may have remained hidden under rocks or vegetation to avoid predation during nights when foraging was not necessary. Daugherty and Sheldon (1982b) observed 10–30 *A. montanus* per survey but estimated the population size to be at least 200–300. Variation in total captures between streams also could be attributed to differences in stream area. Bald Mountain and Lower Jiggs Creeks were higher order streams with much wider channels within sample reaches. Although reach lengths were adjusted for overall area searched within the channel, in general, larger streams had more available within-channel habitat and could have supported larger populations of frogs.

The seasonal pattern of captures within the study area was consistent with that found by others (Metter, 1964; Daugherty and Sheldon, 1982b). Although captures declined markedly in winter, at least some frogs in our study area did not appear to hibernate. Growth data suggested that frogs grew year-round and likely had at least minimal activity throughout the winter. Frogs may have moved out of the stream channel in coastal areas during fall and early winter rains, thus avoiding high stream flows while foraging. Captures may have decreased in winter if frogs had migrated out of the channel and were active and foraging within the forest. Wahbe et al. (2004) found that *A. truei* moved greater than 100 m from the stream channel in both clear-cut and old growth sites. On streams in the Olympic Peninsula of Washington, Noble and Putnam (1931) proposed that *A. truei* moved into the forest following rains, because fewer frogs were found near streams when the vegetation was wet. Metter (1967) reported that adult *A. truei* from coastal populations in Oregon and Washington, usually abundant near the stream during dry weather, were not found near the stream during very wet weather.

Overall, we found significantly more adult males than females in all streams. Emlen and Oring (1977) defined operational sex ratio as the average ratio of sexually active females to males at any given time. Stephenson and Verrell (2003) suggested that the operational sex ratio for *A. montanus* may be skewed toward males because fewer females than males were found throughout the year for populations in northern Idaho. The operational sex ratio is strongly affected by spatial and temporal clumping of the limiting sex. Continuous sexual activity by males and asynchronous sexual activity by females can produce a skew in the operational sex ratio (Emlen and Oring, 1977). Because males appeared to mate annually, whereas females likely had a biennial reproductive cycle, it is possible that the operational sex ratio may have been skewed toward males in our study area. However, we may have found more adult males overall because of a difference in detectability between the sexes. For example, males in search of mates may have been easier to detect (Bull and Carter, 1996), or females may be more difficult to locate during oviposition.

Knowledge of a species' life history is critical for understanding its population dynamics, developing effective management plans, and providing insight into future research objectives (B. R. Noon, I. S. McKelvey, D. W. Lutz, W. S. Lattage, R. J. Gutiérrez, and C. A. Moen, U.S. Department of Agriculture, Forest Service, General Technical Report, PSW-GTR-133, 175-186, 1992). Comparative geographic variation studies throughout the range of *Ascaphus* are needed to aid in understanding life-history and ecological differences both within and among regions. This study has quantified and confirmed life-history traits previously predicted for coastal *A. truei* populations, such as a prolonged growing season resulting in faster growth and a younger age at sexual maturity as compared to inland *Ascaphus* populations. Although limited in geographic scope, our results also provide evidence that, in coastal populations, *A. truei* exhibit a biennial, rather than annual, reproductive cycle. This result has important implications regarding the ability of *A. truei* populations to recover from environmental disturbances. A population with biennially reproducing females may not recover as quickly from disturbances as a population with annually breeding females. Likewise, knowledge of age at sexual maturity is critical for conducting future population studies to help determine which age classes may be most susceptible to potential environmental impacts. Attaining reproductive maturity at a younger age has benefits such as a shorter generation length and greater rate of population increase

(Morrison and Hero, 2003). This life-history trait may, therefore, offset the potential effects of biennial reproduction, relieving females of the energetic costs of annual egg production. Quantifying these and other life-history traits provides key demographic parameters for coastal *A. truei*, which has important implications regarding conservation and management of this species.

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