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VARIATION IN AGE AT METAMORPHOSIS ACROSS A LATITUDINAL GRADIENT FOR THE TAILED FROG, *ASCAPHUS TRUEI*

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ABSTRACT: Tailed frogs (*Ascaphus truei*) occur in permanent, cold streams in northwestern North America. Their tadpoles reportedly undergo metamorphosis after 2–4 years. Coastal populations that we examined transformed in 2 yr from the Olympic peninsula in Washington to northern Oregon, but in 1 yr from central Oregon to northern California. One inland site in northern California had a 2-yr period. Age at metamorphosis was consistent over different years. We suggest that total length and developmental stage accurately define cohorts for larval *Ascaphus*. Hind-leg length indicates whether metamorphs are a separate age class from tadpoles. Age at metamorphosis (1–4 yr) appears to reflect broad differences in climatic conditions. However, at a regional scale, variation is low and suggests a lack of sensitivity to local environmental conditions. This may be due to seasonal constraints on the time when metamorphosis occurs (late summer).

Key words: Anura; *Ascaphus truei*; Tadpoles; Ageing; Size classes; Life history; Metamorphosis; Phenotypic plasticity

TAILED frogs (*Ascaphus truei*) are a distinctive lineage that recently was proposed as a sister group to all other anurans (Ford and Cannatella, 1993; Jamieson et al., 1993). The species occurs throughout the Pacific Northwest of North America (Nussbaum et al., 1983), ranging across environmental regimes from wet and mild in coastal sites (Bury, 1968) to drier, colder conditions in the interior Rocky Mountains (Daugherty and Sheldon, 1982; Metter, 1967). Tadpoles have long larval periods and require permanent, rocky streams that are cool and well oxygenated all year (Corn and Bury, 1989; de Vlaming and Bury, 1970; Noble and Putnam, 1931). These features of *Ascaphus* provide a unique combination for study of larval life-history and adaptation.

Age at metamorphosis in *Ascaphus* has been determined from size classes (using total length) and developmental stage. Metter (1967) examined the length of larval life in 17 populations of *Ascaphus* in Washington, Oregon, Idaho, and Montana. He reported that all coastal populations and most Cascade Mountain populations had a 2-yr larval period, whereas some Cascade Mountain populations (n = 3) and all interior populations (Rocky and Blue mountains) had a 3-yr larval period. He concluded that coastal populations transform in 2 yr based on two samples: the Olympic Mountains (Washington) and the northern Coast Range of Oregon. Metter (1967) always considered metamorphs to be a separate age class.

Brown (1990) faulted Metter's (1967) analysis when he argued that some populations in the Mt. Baker region (north Cascade Mountains, Washington) require 4 yr to reach metamorphosis. He suggested that the cold temperatures and short growing season of that region prolong the larval period. Bury and Corn (1991) found that only one size-class was present in at least four of 29 populations of *Ascaphus* in the Oregon Coast Range, but most of these samples were too small for reliable analysis.

Geographic variation in the larval life history traits of amphibians is extensive and results from both environmental and genetic influences (Berven et al., 1979). For example, the age at metamorphosis of wood frogs (*Rana sylvatica*) increases with elevation but decreases with latitude (Berven, 1982; Berven et al., 1979). Clinal variation in larval life history traits has not been well documented for stream-breeding amphibians, and *Ascaphus truei* is of particular interest as it is the only torrent-breeding anuran in North America.

Here, we determine the length of larval life for *A. truei* over an 800-km latitudinal gradient in coastal Washington, Oregon, and northern California. We examine life history variation among populations and compare samples both within and among years.

Materials and Methods

We captured 2503 larval *Ascaphus* at 10 sites (A–J in Appendix I) in coastal Washington, Oregon, and California (Fig. 1). We obtained 2–3 samples within years (at least 1 mo apart) from nine of the sites, mostly in summer but visits were opportunistic. Most tadpoles were collected using a hand-held seine (hardware cloth approximately 30 × 45 cm) that was held down-current from rocks as they were overturned (Bury and Corn, 1991). Tadpoles were either washed into the seine by the current or we picked them off rocks by hand. This technique yielded tadpoles of all developmental stages ranging from recently hatched to metamorphic individuals.

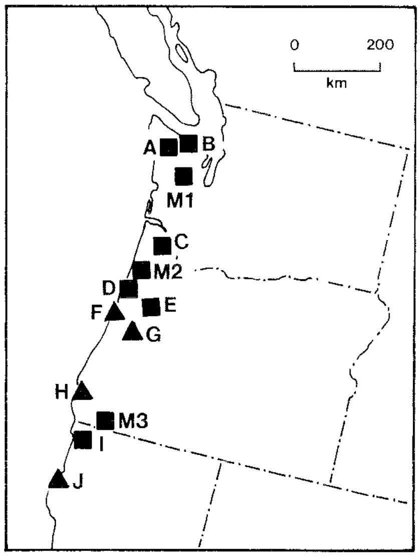

FIG. 1.—Distribution of populations of *Ascaphus* in the Pacific Northwest with 2-yr (squares) and 1 yr (triangles) age-classes. Site locations are for this study (letters) and sites examined by Metter (1967) (M1–M3).

Most tadpoles were released at the site of capture, but we deposited representative vouchers at the National Museum of Natural History, Washington, D.C.; Museum of Vertebrate Zoology, University of California at Berkeley; and U.S. Biological Survey Field Collection, Fort Collins, Colorado.

We measured the total length (TL) and hind-leg length (HLL) of captures, and noted presence of front legs. We separated groups into tadpoles (no front leg) and metamorphs (front legs emerged; stages 42–46: Gosner, 1960). We analyzed TL data of tadpoles using frequency histograms with 2-mm increments and interpreted distinct size-classes to be age classes (following Metter, 1967). We display representative data series in figures; other data are in Table 1. Because resorption of the tail by metamorphs confounds size class analyses, we employed Metter's (1967) decision to treat them as a distinct category in the frequency histograms.

When metamorphs occur in samples, they may be a separate age-class or the

TABLE 1.—Frequencies of total lengths for larval *Ascaphus truei* from coastal regions. M = metamorphic individuals.

Site	Total length (mm) ≤30	32	34	36	38	40	42	44	46	48	≥50	M	*n*
Washington													
A. Cougar Creek, 19 July 1995	6	8	19	17	4	3			3			11	71
Cougar Creek, 28 Sept. 1995	1	3	13	22	31	35	8	1	2			1	117
Oregon													
C. Quartz Creek, 15 Aug. 1991			6	12	25	13	8					24	64
Quartz Creek, 15 Aug. 1992			2	2	3	13	16	15	5			18	74
Quartz Creek, 7 Aug. 1996			2	18	39	55	36	20	8			33	211
D. Schooner Creek, 17–18 Aug. 1992				1		4	16	30	27	16	4	103	201
Schooner Creek, 6 Aug. 1996					3	6	13	14	11	6	3	22	78
F. Ten Mile Creek, 13 April 1985	4			3	3	10	17	8	2				47
Ten Mile Creek, 13 April 1989				2	2	3	5	5	4	1			22
Ten Mile Creek, 27 June 1986						2	3	11	3			16	35
G. Smith River, 31 March 1987			7	6	12	15	13	3	4				60
Smith River, 8 May 1985				5	11	18	13	1					48
Smith River, 25 June 1986							3	9	15	16	5	13	62
H. Dry Run Creek, 1 June 1991							1	1	2	4	23		31
Dry Run Creek, 12 Aug. 1991							1					34	35
California													
I. French Hill Creek, 18–31 July 1996	2	3	16	27	28	8	3	1				5	93
French Hill Creek, 24–29 Aug. 1966	8	5	20	30	18	8	7	1		1		3	101
J. Grahams Gulch, 18 March 1962	24	1	1		4	1							31
Grahams Gulch, 1 April 1962	20	4	2	1									27

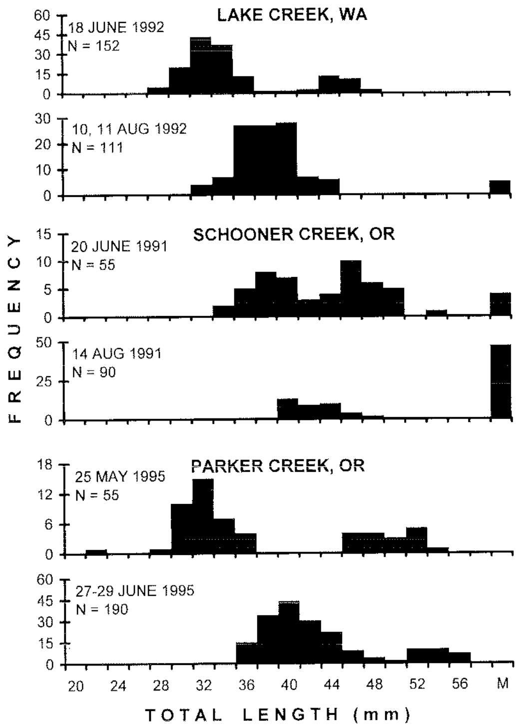

FIG. 2.—Total length or metamorphic status (M = metamorphosing) of larval *Ascaphus* from populations with 2-yr larval periods. Note that the Y-axis scale differs among histograms.

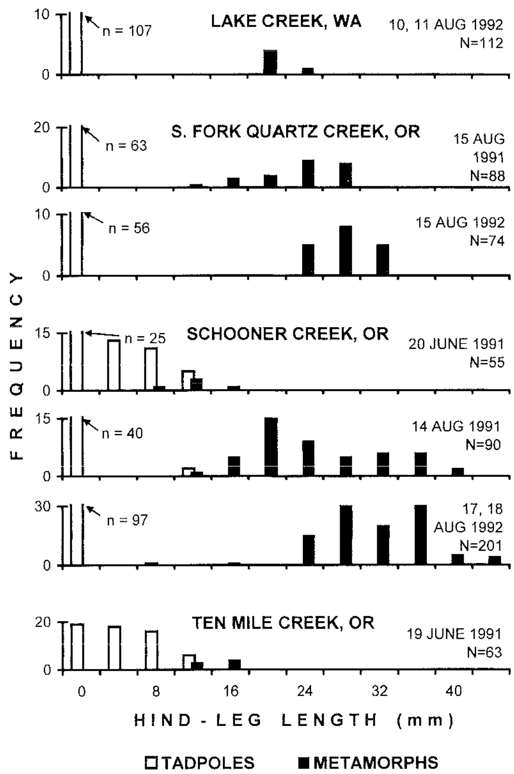

FIG. 3.—Hind-leg length of metamorphs versus tadpoles of *Ascaphus*. Note that the Y-axis scale differs among histograms. When hind-leg lengths overlap, we conclude that tadpoles and metamorphs are one age-class.

same age as the largest size-class of tadpoles. They were compared to the largest size-class of tadpoles using HLL histograms. Overlap in HLL between metamorphs and the largest size-class of tadpoles was considered evidence that both groups are in the same age class. Nonoverlapping HLL's suggest that metamorphs may be a separate age class.

Tadpoles of *Ascaphus* may hatch from eggs in late summer while the oldest cohort is completing metamorphosis (Adams, 1993; Brown, 1990). Thus hatchling larvae are considered as age zero and are not counted as an age class.

Finally, we compared size of first-year tadpoles to latitude, elevation, and aspect (degrees deviation from North) using Pearson correlations and Bonferroni-corrected probabilities generated with SYSTAT 7.0. All but one of the samples analyzed were collected between 18 June and 19 July. The exception was a sample from 1 June at Dry Run Creek (H), which was included to increase geographic coverage.

RESULTS

Two populations of *Ascaphus* in coastal Washington and three sites in northwest Oregon (Fig. 1A–E) appeared to have a 2-yr larval period. Cougar Creek (A), Lake Creek (B), and Schooner Creek (D) all had two size classes of tadpoles in midsummer, one of which transformed in August (Table 1, Fig. 2). A June sample at Schooner Creek indicates that metamorph HLLs overlap with HLLs of the larger of two-size classes of tadpoles present in midsummer (Fig. 3). At both Lake and Schooner creeks, HLL frequency distributions of metamorphs and tadpoles show a large gap between the two groups in August (Fig. 3).

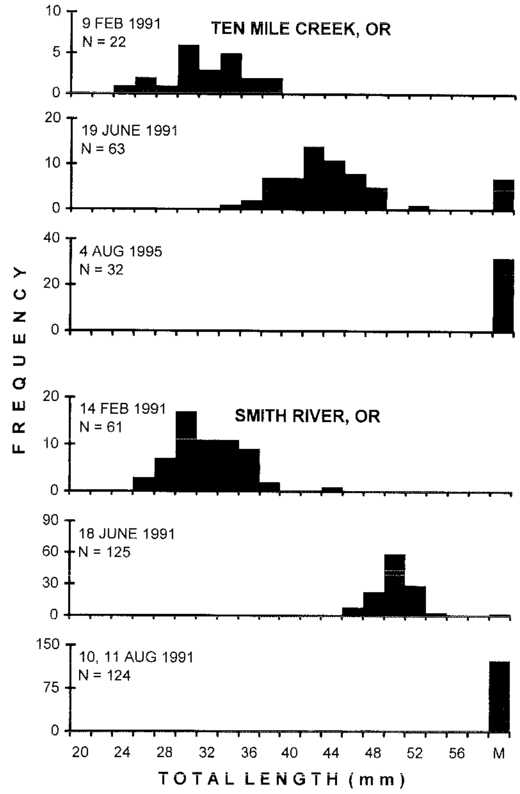

FIG. 4.—Total length or metamorphic status (M = metamorphosing) of larval *Ascaphus* from populations with 1 yr larval periods. Note that Y-axis scale differs among histograms.

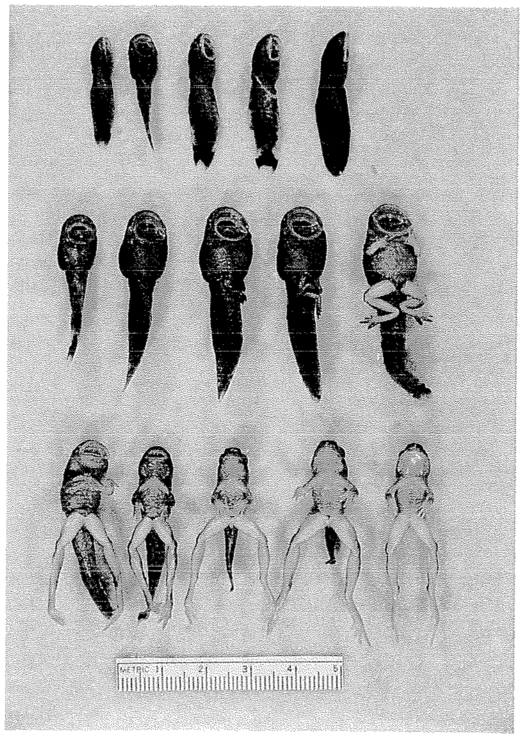

FIG. 5.—Tadpoles and metamorphs of *Ascaphus* from Smith River, Oregon (1 yr larval period), in 1991: February (top), June (middle), and August (bottom). Each series shows the range of variation within the monthly sample.

Quartz Creek (C) in north coastal Oregon had one size class of tadpoles plus metamorphs in August of 1991, 1992, and 1996 (Table 1). Tadpole HLLs were distinct from metamorphs in all years (e.g., Fig. 3). We collected two samples at Parker Creek (E) in the Oregon Coast Range, and both had two age-classes of tadpoles (Fig. 2).

We obtained six samples each from Ten Mile Creek (F) on the coast and Smith River (G) in the Coast Range, Oregon (Table 1, Fig. 4). Tadpoles formed a single size class in February, and all transformed in August (Fig. 4). In June samples, tadpoles and metamorphs appeared as a single age-class because all tadpole HLLs were continuous from 0–19 mm (e.g., Fig. 3). There was marked variation in the developmental stages of individual tadpoles within samples (Fig. 5), but tadpoles at both sites all metamorphosed by the end of the summer (about 1 yr since hatching from eggs). Samples collected in other years at Ten Mile Creek and Smith River all appear to have a 1 yr larval period (Table 1). Two samples from Dry Run Creek (H) in south coastal Oregon show a single age-class in 1991 (Table 1). All but one tadpole were transforming in the August sample. However, small sample sizes make conclusions equivocal.

In California, we obtained data at two sites. There appear to be two age classes at French Hill Creek (I) in coastal foothills: mostly tadpoles with a few metamorphs in summer months (Table 1). HLL was not measured here, but the large number of tadpoles in late August suggests at least a 2-yr larval period. Small samples taken in spring from Graham's Gulch (J) in a coastal area are inconclusive (Table 1).

TABLE 2.—Pearson correlations (lower triangles) and Bonferroni corrected *P*-values (upper triangles) comparing tadpole TL after approximately 1 yr of growth with three predictor variables; $n = 10$ sites including French Hill Creek which is excluded as an outlier in the second matrix.

	TL	Latitude	Elevation	Aspect
French Hill Included				
TL	—	0.260	0.570	1.000
Latitude	−0.647	—	0.219	1.000
Elevation	−0.556	0.663	—	1.000
Aspect	0.161	−0.056	−0.204	—
Without French Hill Creek				
TL	—	0.002	0.418	1.000
Latitude	−0.924	—	0.259	1.000
Elevation	−0.629	0.682	—	1.000
Aspect	0.064	−0.294	−0.285	—

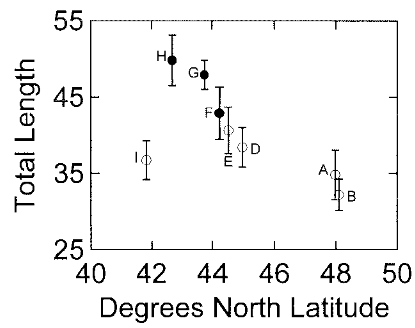

FIG. 6.—Total length (mm) of larval *Ascaphus* after approximately 1 yr of growth. Data are from June and July samples. Error bars show ±1 SD and represent within-sample variation in all cases except sites G and F that had samples from 2 yr. G: 25 June 1986 ($\bar{x}$ = 46.5, SD = 2.153) and 18 June 1991 ($\bar{x}$ = 49.3, SD = 1.894). F: 27 June 1986 ($\bar{x}$ = 43.6, SD = 1.710) and 19 June 1991 ($\bar{x}$ = 42.1, SD = 3.446). Filled circles are 1 yr larval periods.

After 1 yr of larval development, TL of tadpoles had negative correlations with latitude and elevation, and they had a positive correlation with the degrees deviation from a North aspect (Table 2). Latitude and elevation were correlated with each other in this analysis ($r = 0.663$, Table 2). French Hill Creek was an outlier (Fig. 6) and its exclusion caused the correlation between TL and latitude to become significant (df = 8, corrected $P = 0.002$, Table 2).

DISCUSSION

We provide the first documentation of 1 yr larval periods for *Ascaphus truei*. Length of larval life (either 1 or 2 yr) appeared consistent over different years. Although Metter (1967) reported that coastal populations of *Ascaphus* transform in 2 yr, his two coastal sites (sites M1 and M2, Fig. 1) were both north of the region where we found 1 yr larval periods. Our data are consistent with a 2-yr larval period from north coastal Oregon to the Olympic peninsula in Washington. However, we did not sample the Willapa Hills, a small coast range in southwestern Washington where *Ascaphus* was recently discovered (Adams and Wilson, 1993).

We found that single age-classes in midsummer samples sometimes had tadpoles with a wide range of developmental stages (Fig. 5). In small samples, developmental variation may appear to represent more age-classes than actually exist. Assigning tadpoles to developmental categories (e.g., Bury and Corn, 1991) can roughly document the range of variation but may be misleading in defining age-classes. Metter (1967) and Daugherty and Sheldon (1982) assumed that metamorphs always represent a separate age-class. However, some summer samples of coastal populations have metamorphs that are in the same age-class as tadpoles. As noted by Metter (1967), it is obvious whether metamorphs are a separate age-class with animals in hand, but animals collected are often released and the use of HLL helps increase the objectivity of the analysis. Conclusions derived using HLL to determine whether metamorphs are a separate age class were the same as conclusions derived from other samples when HLL was not needed. This held true for two populations where both types of sample were obtained (Lake Creek and Ten Mile Creek).

Occasional outliers (tadpoles with sizes that do not fit with the rest of the sample) may represent atypical development rather than cohorts that were missed, because all sizes of tadpoles are readily collected when they are present. However, stochastic events such as floods could sometimes remove most of a cohort (Metter, 1968). Also, a small portion of a cohort may over-winter an additional year, but this would be difficult to detect without large samples at different times of the year. For example, one tadpole at Schooner Creek (14 August 1991, Fig. 3) had HLL similar to metamorphs. It appears to be the same age as metamorphs, but we do not know if it reached metamorphosis that year. In general, we conclude that age at metamorphosis can be accurately measured for coastal populations of *Ascaphus* by using frequency histograms of TL and HLL for samples of ≥50 tadpoles and metamorphs. Larger sample sizes may be necessary in inland regions to distinguish between 3- and 4-yr larval periods.

Reported ages for metamorphosis of *Ascaphus* now range from 1 yr (this study) to 4 yr (Brown, 1990). The longest larval periods (3–4 yr) occur in inland or high elevation areas with short growing seasons. The 2-yr larval periods occur in northern coast ranges and the Cascade Mountains of Washington and Oregon, and the Siskiyou Mountains of southern Oregon and northern California (Fig. 1). One year larval periods in Oregon are found in central and south coastal sites and the nearby Coast Range, which is the region with the warmest year-round temperatures and the longest growing season in the Pacific Northwest (Franklin, 1988). Similar mild conditions exist in north coastal California where *Ascaphus* may also have a 1 yr larval period. Thus, the 1 yr larval period is known only from coastal sites or nearby where maritime conditions result in a relatively mild climate (e.g., little or no freezing in winter).

With the exception of French Hill Creek (I), tadpole size after approximately 1 yr of growth was most closely associated with latitude (Fig. 5). However, the correlation between latitude and elevation makes conclusions equivocal. One year tadpoles at French Hill Creek were relatively small, which is consistent with other populations having 2-yr larval periods rather than with populations from similar latitudes. If embryo size is assumed constant, this pattern suggests that there is an unknown environmental factor slowing growth at French Hill Creek. Nearby high mountains (Siskiyous) may result in relatively cold waters and slow growth at this site.

That age at metamorphosis appears consistent over broad regions (e.g., Rocky Mountains) led Metter (1967) to suggest that this trait may be genetically determined. Because amphibian development is sensitive to temperature (Smith-Gill and Berven, 1979), food availability (Berven and Chadra, 1988; Kupferberg et al., 1994), and predators (Skelly and Werner, 1990), it is surprising that more local variability in age at metamorphosis has not been observed. However, genotypic and phenotypic effects are difficult to separate (Berven et al., 1979; Roff, 1992, Stearns, 1992). It would be premature to conclude that genotypic fixation of metamorphic age has occurred. Rather, larval life in *Ascaphus* could be a phenotypic response to temperature (i.e., degree days) but still show little variation in age at metamorphosis. Metamorphosis in *Ascaphus* appears constrained to a relatively short period in late summer, which may mask local variation in developmental rates. When seasonally restricted, metamorphosis should occur at smaller sizes as degree-days decrease until it becomes more advantageous to risk another year of growth in the larval environment (Roff, 1980; Werner, 1986; Wilbur and Collins, 1973). Thus, local developmental variation may appear as changes in size at metamorphosis rather than age unless environmental differences are extreme.

Knowledge of life-history variation aids our understanding of how species interact with their environments. The discovery of 1 yr larval periods demonstrates greater capacities for growth and adaptation in *Ascaphus* than previously thought. It raises the possibility that some south coastal populations might be able to adapt to streams that partially dry by the end of summer or early fall. For example, the tributary of Smith River (G) was reduced to a few isolated pools in September 1984 and August 1992. Fitness in these conditions may be higher for tadpoles able to transform before summer drought. Thus, the ability to metamorphose after 1 yr of larval development may allow persistence of *Ascaphus* in parts of its range.

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Appendix I

Descriptions of Study Sites

WASHINGTON—(A). COUGAR CREEK, 21 km SW Port Angeles, Olympic National Park, Clallum Co., flows NE; 2–3 m wide; 610 m elev.; 47°59′N. Lat. (B). LAKE CREEK, 2 km S Heart-of-the-Hills campgrd., Olympic National Park, Clallum Co.; flows NE; 2–3 m wide; 630 m elev.; 48°01′N. Lat. **OREGON**—(C). SO. FORK QUARTZ CREEK, 8 km SE of Elsie, Washington Co.; flows N; 1–2 m wide; 350 m elev.; 45°50′N. Lat. (D). SCHOONER CREEK, 9.5–14.5 km E Lincoln City, Lincoln Co.; flows WSW; 3–4 m wide; 110 m elev.; 44°57′N. Lat. (E). PARKER CREEK, 16 km WSW Philomath, Benton Co.; flows SW; 2–3 m wide; 745 m elev.; 44°30′N. Lat. (F). TEN-MILE CREEK (tributaries), 3.4 and 3.9 km E Hwy 101, Lane Co.; flows S; 1 m wide; 85 m elev.; 44°13′N. Lat. (G). TRIB. of SOUTH FORK SMITH RIVER, 16 km NW Drain, Douglas Co.; flows N; 1–2 m wide; 245 m elev.;

43°45′N. Lat. (H). DRY RUN CREEK, Humbug Mountain State Park, Curry Co.; flows SW; 1–2 m wide; 35 m elev.; 42°41′N. Lat. **CALIFORNIA**—(I). FRENCH HILL CREEK, 3.5 km WSW Gasquet, Del Norte Co.; flows N; 1–2 m wide; 185 m elev.; 41°50′N. Lat. (J). GRAHAM'S GULCH, 11 km ESE Eureka, Humboldt Co; flows W; 1–2 m wide; 30 m elev.; 40°45′N. Lat.