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Population Structure, Growth, and Size of Larval *Dicamptodon ensatus* (Eschscholtz)

The Pacific giant salamander, *Dicamptodon ensatus* (Eschscholtz), is a characteristic and dominant element of the salamander fauna of the western Coniferous Forest Biome. Although known to herpetologists since 1833, its life history is poorly understood. Rathke (in Eschscholtz, 1833) found a shrew in the stomach of the holotype; and since that time the remarkably voracious feeding habits of both the larvae and transformed individuals have been repeatedly confirmed. Cope (1889) established the fact that some individuals are neotenic. Little else of significance concerning the life history of *D. ensatus* appeared in the literature until the studies of Henry and Twitty (1940), Kessel and Kessel (1943a, 1943b, 1944), and Dethlefsen (1948) led to an hypothetical life history. Briefly, the proposed life cycle is as follows. The salamanders breed in the spring. Eggs are deposited underground in the heads of springs. Development is slow, and hatchlings do not appear until late fall or winter. Kessel and Kessel (1943a), following Storer (1925), state that the young hatch at 17 mm total length. Earlier, however, Henry and Twitty (1940) showed that Storer's data were based on hatchlings of the northwestern salamander, *Ambystoma gracile* (Baird) and not *D. ensatus.* Kessel and Kessel (1943a) estimated growth rates of larvae to be 7.58 to 12.34 mm total length per month through their first summer, attaining a total length of about 100 mm one year after hatching. Larvae continue to grow into their second summer and transform from June to August at total lengths of about 135 mm. Kessel and Kessel (1944) speculated that some individuals may not transform during years of unusually high precipitation, and that these individuals may become sexually mature larvae.

Recent field work with populations located throughout the range has shown that there is considerable, and to some extent predictable, variation in the life history of *D. ensatus.* Information on variation in population structure, growth, and size of larval *D. ensatus* is presented in this paper.

Larval Habitat

Valentine and Dennis (1964) recognized three ecological types of salamander larvae: mountain brook dwellers, stream dwellers, and pond dwellers. Earlier workers (e.g., Dunn, 1926) recognized only two categories, lumping the mountain brook and stream types and using the terms interchangeably. Noble (1931) and others placed *D. ensatus* in the lumped category, while Valentine and Dennis (1964) more specifically placed *D. ensatus* in the mountain brook category. While their classificatory criteria are primarily morphological, the term "mountain brook" in reference to *D. ensatus* is somewhat misleading. Larvae are found in a greater variety of habitats than is generally believed. They are too numerous in many lakes and ponds to be considered accidentals, and they are found in all types of lotic environments from the smallest mountain brook or seepage to fairly large rivers. As will be shown below, the wide variety of aquatic habitats occupied by populations of larval *D. ensatus* is paralleled by variation in population structure.

Population Structure

The structure of stream-dwelling populations of larval *D. ensatus* seems to depend to a large extent on the size and flow-regime of the stream occupied. Populations of larval *D. ensatus* in five general, intergrading categories of streams will be described below. The five categories are: (1) regularly intermittent, (2) potentially intermittent, (3) small permanent, (4) medium-sized permanent, and (5) large permanent.

Because embryos are prefeeding for about nine months (Nussbaum, 1969), and because the larvae require at least one year of growth before they metamorphose, regularly intermittent streams are lethal habitats. Larvae are rarely found in these streams.

Some small, spring-fed streams stop flowing only during exceptionally dry years. These potentially intermittent streams often support populations of larval *D. ensatus* which seem to be structured similarly to larval populations found in small permanent streams (see below). These populations are, however, subject to extinction in dry years, as has been witnessed on two occasions. On 15 May 1969, many first-year larvae (a sample of 85 averaged 51.3 mm total length, range 48.1 to 55.6 mm) were seen in a 100-foot section of a small tributary of Parker Creek, Lincoln Co., Oregon. The tributary was completely dry on 30 July 1969, and the population was presumed to be defunct. A similar situation occurred during the very dry summer of 1967 in a small, unnamed stream on the north side of Mount Pilchuck, Snohomish Co., Washington. This latter stream was seen to be repopulated in the summer of 1969, and had not suffered extinction through the summer of 1972.

There are usually two size-classes (age-categories) of larval *D. ensatus* present in small, premanent streams during the spring and early summer. By midsummer flow is greatly reduced, and individuals in their second year begin to transform. By late summer and fall only one size-class remains, those still in their first year of growth. A few second-year larvae may remain one more winter to transform in their third summer, but neotenes are rare in these streams. This is essentially the situation described by Kessel and Kessel (1943a, 1943b) for a population in Corte Madera Creek, Marin Co., California (Fig. 1), and is exemplified by populations in China Gulch, near Gualala, Mendocino Co., California, and in small tributaries of Fall Creek, Lincoln Co., Oregon (Fig. 2A and 2B).

More detailed data are available for a population in a small permanent spring on Gauldy Mountain, Tillamook Co., Oregon. This spring originates near the top of a north-facing slope, flows for 405 feet, and then ends in a small pool on a bench-like area. The closed nature of the spring creates an ideal situation for a population study. Numbered stakes were placed along the stream at five-foot intervals. Each month beginning in mid-March, 1965, and ending in mid-February, 1966, the stream was systematically worked from the lower end up to the origin. Larvae were captured, their position by stake number noted, measured, marked, by toe clipping, and released. Population structure, rate of growth, time of year of metamorphosis, dispersion of larvae, and flow-regime are summarized in Figure 3 and Table 1.

The number of first-year larvae present in March, 1965, was estimated at 246 (s.e. = 36) by the Peterson Index method. There were 105 (s.e. = 15) second-year larvae present the same month. Therefore, each 100-foot section of stream had 61 first-year larvae and 26 second-year larvae, or 87 individuals per 100 linear feet of stream. The ratio 61-26/61 provides an estimate of the mortality rate (57 percent) for the first year of larval life. This method of estimation assumes a stable

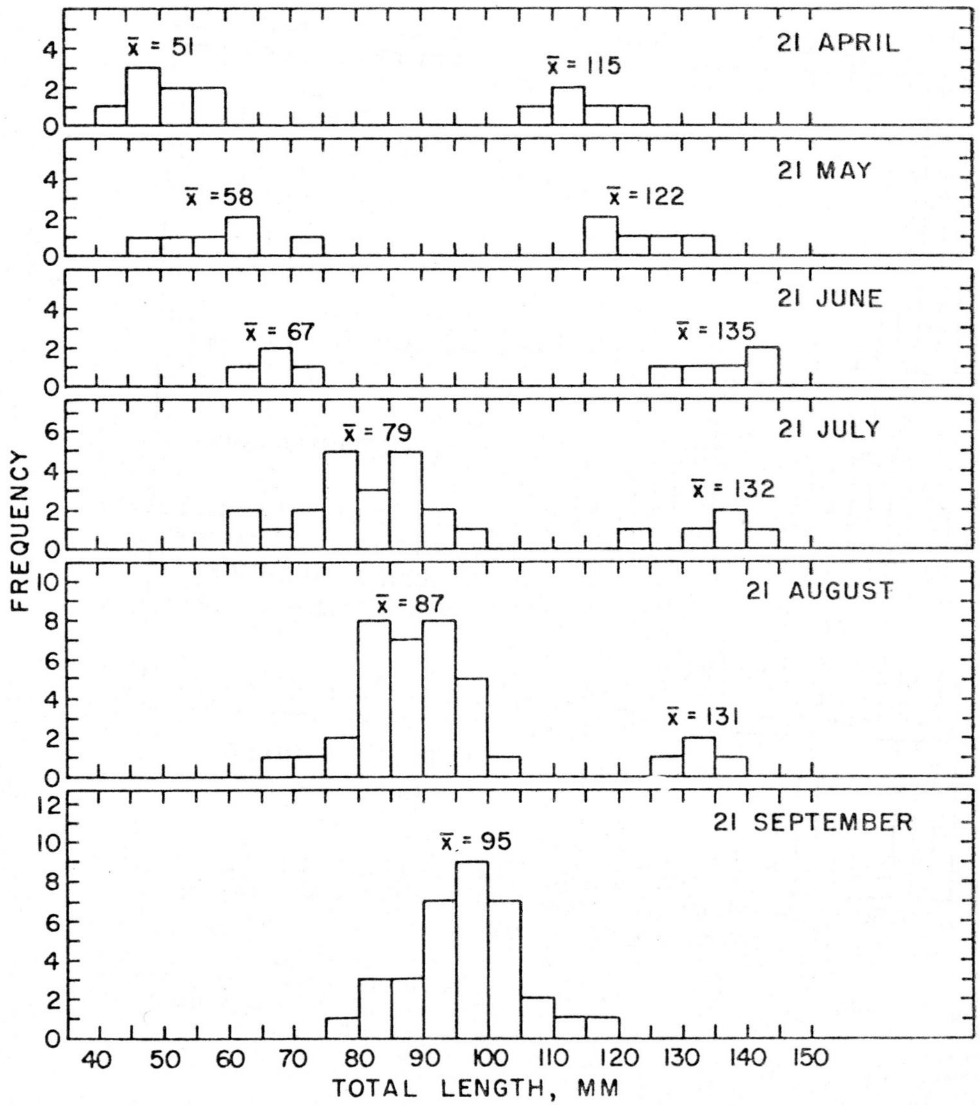

Figure 1. Population structure and growth of larval *D. ensatus* in Corte Madera Creek, Marin Co., California. Drawn from data presented by Kessel and Kessel (1943a, 1943b).

population, an assumption which is not always valid; however, monthly sampling of the first-year group (Fig. 3) suggested that a mortality rate of 50 to 60 percent is not unrealistic. It is interesting, but perhaps fortuitous, that Bannikov (1949), using a similar method, calculated the mortality rate of first-year, larval *Ranodon sibiricus,*

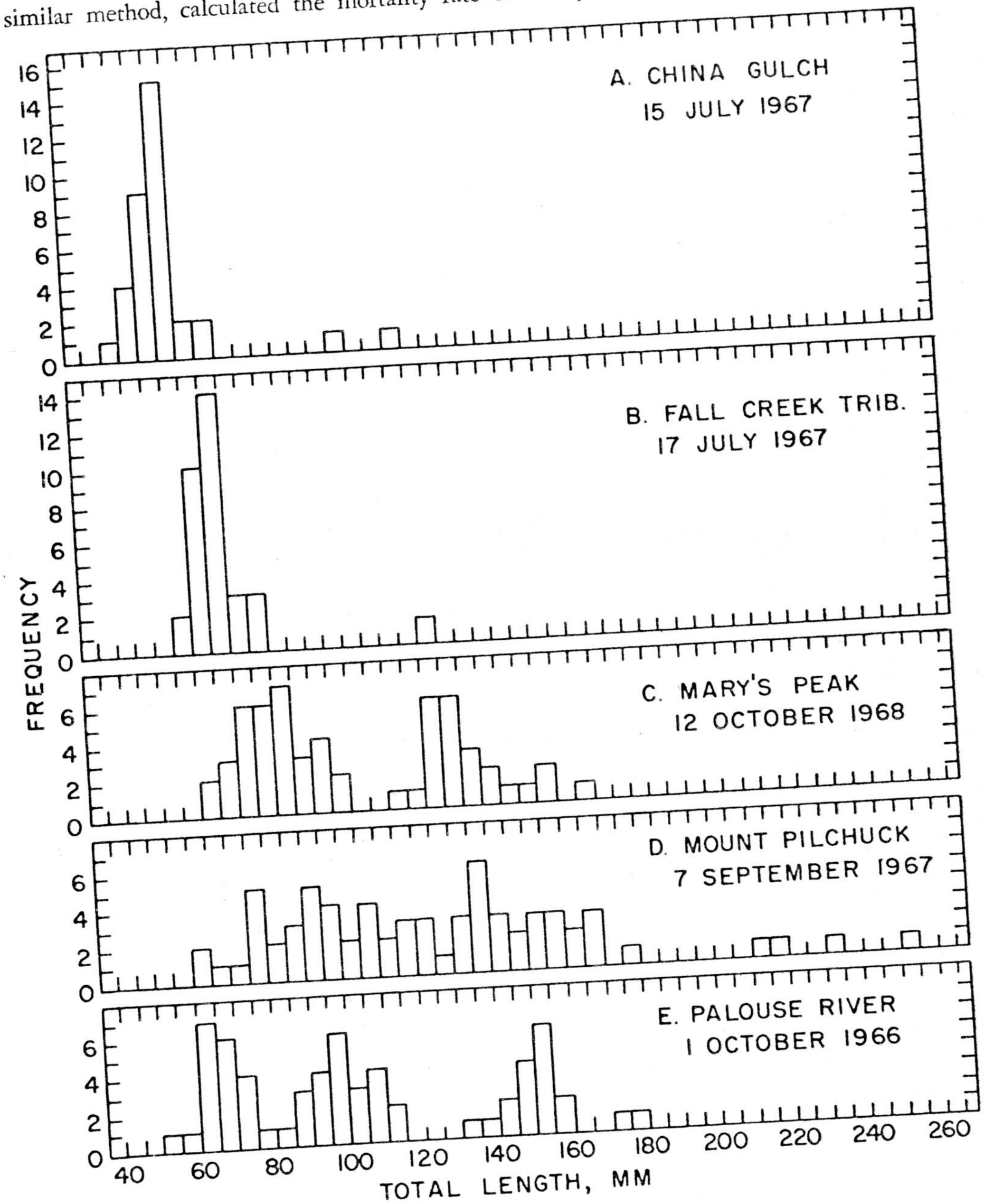

Figure 2. Frequency distribution of sizes of larval *D. ensatus* in different habitats. A and B are small streams, C and E are streams of intermediate size, and D is a large stream. Second-year larvae transform early in small streams, but are still present in the fall months in intermediate- and large-sized streams. The Palouse River population occurs in a harsh climate, which may partly explain the trimodality (see text).

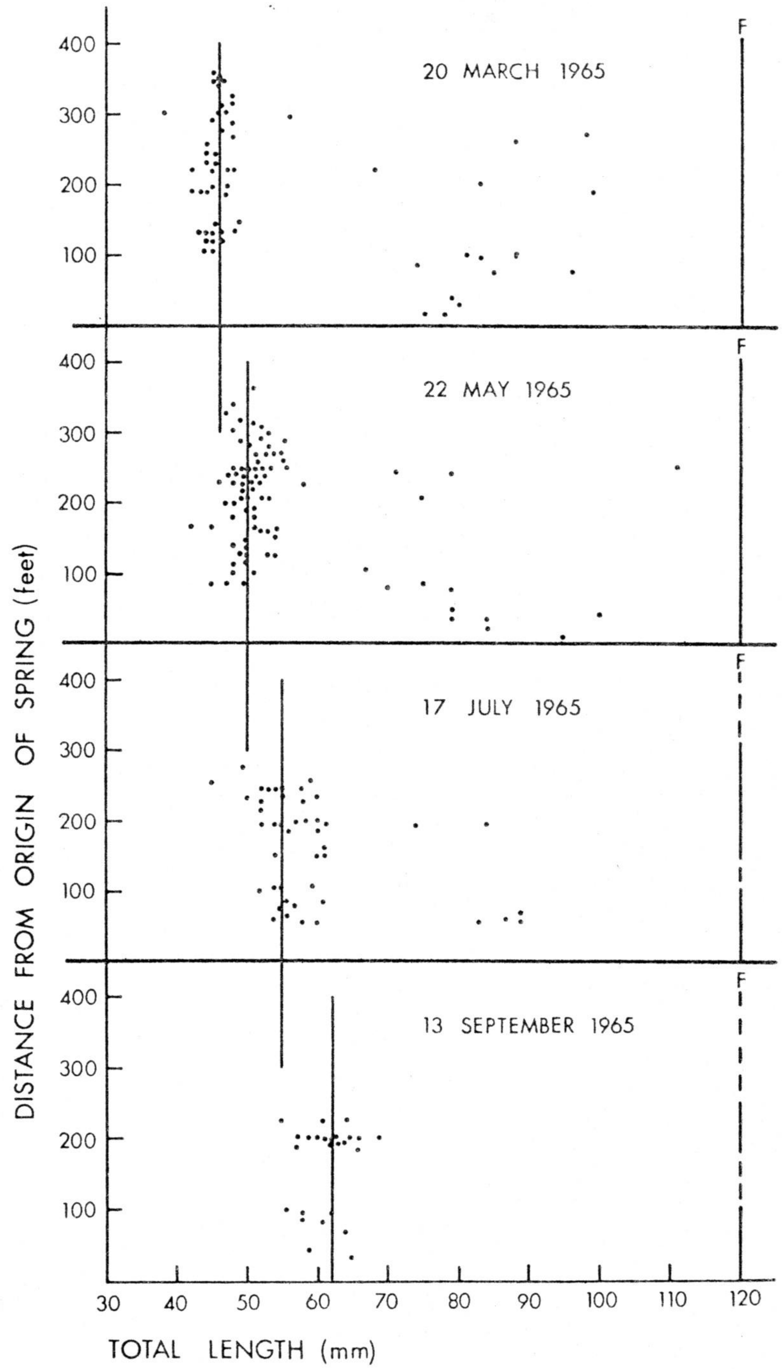

Figure 3. Summary of a population study of larval *D. ensatus* on Gauldy Mountain, Tillamook Co., Oregon. Dots represent single individuals. Two size-classes are evident. Vertical line through first-year class represents mean total length. Line F represents stream flow; surface flow where solid, subsurface where dashed. Note dispersion of larvae in relation to flow-regime, decreasing numbers of second-year larvae due to metamorphosis, and growth of first-year larvae (also see Table 1).

TABLE 1. Growth of first-year larvae at Gauldy Mountain, Tillamook County, Oregon.

Sampling date	Mean total length (mm)	Standard error	Maximum-minimum (mm)	Mean increase (mm)	N
3/30/65	45.7	.40	56-38	—	43
4/23/65	46.6	.28	52-38	0.9	83
5/22/65	50.3	.31	58-42	3.7	82
6/19/65	53.1	.39	62-47	2.8	61
7/17/65	55.7	.60	61-45	2.6	40
8/14/65	58.4	.72	68-48	2.7	36
9/13/65	61.7	.94	74-50	3.3	25
10/10/65	60.2	.93	69-55	−1.5(?)	15
11/14/65	63.0	.79	65-60	2.8	7
2/26/66	45.7	.50	49-41	—	17

a stream-dwelling hynobiid, to be 57.3 percent; and Bruce (1972) estimated the annual mortality of larval *Pseudotriton ruber,* a spring- or stream-breeding plethodontid, at about 50 percent.

Causes of mortality are primarily predation (including cannibalism) and desiccation. Mortality is highest in mid and late summer when flow is reduced (Fig. 3). At this time the larvae are concentrated, and crowding leads to a higher incidence of cannibalism and greater exposure to predators. Eventually many succumb to desiccation as isolated pools become smaller.

By July the number of second-year larvae was drastically reduced (Fig. 3), and in September none was collected. Only a few were collected in later months. Although some may have died, we believe that most metamorphosed and deserted their diminishing aquatic habitat. Five individuals collected in June and July were in the process of metamorphosing.

A different situation exists in permanent streams of medium size. Flow is reduced in late summer, but enough water is present to provide adequate food and cover for the larger second-year larvae throughout the year. A stream on Mary's Peak, Benton Co., Oregon, typifies this situation (Fig. 2C). In such streams larvae of two size-classes, including second-year larvae in all stages of metamorphosis, can be found as late as November. Many larvae do not transform until their third summer. The few largest individuals on the extreme right of the histogram are probably third-year larvae. Older, neotenic individuals are occasionally found in streams of this size, but metamorphosis is the rule.

Figure 2E illustrates the distribution of sizes of larvae in a tributary of the Palouse River, Benewah Co., Idaho. This too is a medium-size, permanent stream, but as can be seen from the histogram, the size distribution is different from the Mary's Peak population. Apparently growth is slower at the Palouse site so that three size-classes are present, and metamorphosis occurs only during or after the third year. Many individuals in the third size-class were in the process of metamorphosing when collected. The Palouse site is geographically isolated from the main, coastal portion of the range. Away from the maritime influence, the climate is harsh and the growing season short. The short growing season combined with possible genetic differences may account for the slower rate of growth at the Palouse site.

Large permanent streams which flow strongly throughout the year support populations containing terrestrial adults and neotenes. A large creek on the north slope of Mount Pilchuck, Snohomish Co., Washington, is such a stream. Larvae of all sizes (Fig. 2D) can be found in the stream; and no distinct size-classes are present. In the histogram, the largest individuals to the extreme right are neotenes. There are more neotenes present than is indicated by the histogram, but they are difficult to collect by hand (the method used) because they hide in relatively inaccessible places as compared with smaller larvae. Their abundance is revealed by luring them from their lairs in deep pools and behind waterfalls with baited lines.

Although no proof exists, we suspect the lack of modality is related to the abundance of neotenes in the population. In populations where terrestrial adults supply the eggs, breeding is most likely timed to the fall and/or spring rains when ripe adults migrate to the streams. Neotenes never leave the streams; hence breeding may be asynchronous. There is good evidence from breeding records to support this hypothesis (Nussbaum, unpubl.).

We have no comparable data for lake or pond dwelling populations of *D. ensatus*. However, one often-observed feature of these populations is the high frequency of neotenes. Apparently the lentic environment is conducive to neoteny in this species.

Growth Rates

Average increase in total length per month is given in Table 1 for first-year larvae of the Gauldy Spring population. The highest growth rate, 3.7 mm, is from late April to late May. Kessel and Kessel (1943a) estimated growth rates for first-year larvae in Corte Madera Creek, Marin Co., California, to be 7.58, 8.52, 12.34, 8.21, and 7.87 mm per month for May, June, July, August, and September, respectively. These rates are all higher than those for the Gauldy Mountain population.

In the Mary's Peak population (Fig. 2C) there is a difference of 50 mm between the modes of the two size-classes. This situation suggests an average increase of 4.16 mm per month for the 12-month season. Corresponding values for the Palouse population (Fig. 2E) are 35 mm difference for an average growth rate of 2.92 mm per month.

Size of Larvae

All references to size of hatchlings to date stem from Storer's (1925) report of 17 mm total length. Henry and Twitty (1940) showed Storer's data to be in error, but subsequent authors (e.g., Kessel and Kessel, 1943a; Dethlefsen, 1948) have apparently overlooked the correction.

Embryos hatched from eggs cultured in the laboratory (Nussbaum, 1969) at total lengths of 33.3 to 35.5 mm ($\overline{x} = 34.42$), or at snout to anterior edge of vent lengths of 18 to 19 mm ($\overline{x} = 18.25$). However, when the embryos left their gelatinous membranes, much yolk remained so that they did not feed for another three to four months depending on ambient temperature. When feeding began, the larvae were 45.5 to 51.1 mm ($\overline{x} = 47.24$) total length and 24 to 28 ($\overline{x} = 25.43$) snout-vent length.

There are many vague statements in the literature concerning the maximum size of *D. ensatus* larvae. It is generally stated that they approach or slightly exceed 300 mm total length. The largest specimen actually reported seems to be a 286 mm

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total length neotene from Clackamus Co., Oregon (Bishop, 1943). We know of numerous specimens which greatly exceed this size, the largest being a neotene collected 19 September 1970 in the Columbia River Gorge by the senior author. The live measurements were: snout to posterior edge of vent 205 mm, and total length 351 mm. To our knowledge, this is the longest reported nonfossil, ambystomatid salamander. The previous record was an adult *Ambystoma tigrinum* with a snout-vent length of 164.2 mm and a total length of 346 mm (Smith and Reese, 1968). The latter specimen was captured as a neotene and kept for 15 months in captivity, during which time it transformed and grew 65 mm in total length. Measurements for the neotenic *D. ensatus* were taken the day of capture.

Size of Transformation

If larvae are to transform, they usually do so at 92 to 166 mm total length. Both individual and population variations are known, and it is likely that fluctuations of environmental parameters affect the time and size of metamorphosis.

The largest transforming larva found in nature was 166 mm total length (93 mm snout-vent). Larvae larger than this are well on their way to becoming neotenic and are not likely to metamorphose, although they are not insensitive to thyroid treatment (unpubl. data).

Reed (1949) mentions a transformed individual 96.5 mm total length from coastal Oregon. The smallest naturally transformed specimen we know of (RAN-5140) is 53 mm snout to anterior edge of vent and 92.5 mm total length. The animal was collected on Skamokawa Creek, Wahiakum Co., Washington.

Kessel and Kessel (1943b) found that second-year larvae in Corte Madera Creek began transforming in June and July at total lengths of about 135 mm. At Gauldy Mountain the size at transformation was smaller (95 to 120 mm total length), even though the time of transformation was the same. Individuals in the China Gulch and Fall Creek populations transformed at total lengths of 100 to 120 mm. Corresponding values for the Mary's Peak population were 120 to 150 mm, and 130 to 166 mm for the Palouse population. Only three transforming individuals were collected at Mount Pilchuck, and these were 119, 125, and 129 mm total length.

Discussion

In order to assess accurately the functional role of a species in a community or an ecosystem, it is necessary to understand the basic life history of the species in question. Attempts to model consumer dynamics must take into account variation in population characteristics across space and time; and to the extent that the total range of variation is known for a given species, or that the variation is predictable, models of consumer populations can be designed to account for the variability.

It is clear from the results of this study that populations of larval *D. ensatus* exhibit considerable variation in population structure. However, it appears that much of the variation can be explained or predicted from knowledge of the type of aquatic environment under consideration. Neoteny is apparently advantageous in permanently aquatic sites such as large streams and lakes. In small streams which occasionally dry up, metamorphosis normally occurs, and this facilitates rapid repopulation of a stream by the surviving, terrestrial adults after a period of extreme drought when all larvae are destroyed.

The genetic basis for neoteny and other variable population characteristics such as growth rate, size at metamorphosis, and size (age) when sexually mature is unknown. Some of the variation may be attributed to genetically fixed adaptations to particular conditions in different parts of the range (obligate or geographic variation). But adaptability to different microhabitats or fluctuating ecological factors within a given area is also apparent (facultative variation). This wide range of adaptation and adaptability allows the species to utilize most of the available aquatic habitats in the mountainous regions of the Pacific Northwest and northwestern California. From this point of view, *D. ensatus* appears as an ecologically generalized species (eurytopic) rather than a specialized mountain brook form as is often stated. The ability of the larvae to survive in such a wide variety of aquatic habitats may be a reflection of the historical events (largely unknown) which have allowed *D. ensatus* to enjoy a relatively competition-free existence. In the humid forested regions of eastern North America, larvae of at least 13 species of desmognathine and hemidactyliine salamanders compete for resources associated with small streams and seepages, and the larger streams are inhabited by large, permanently aquatic salamanders such as *Cryptobranchus alleganiansis* and several species of *Necturus*. The lotic environments of eastern North America usually support larval populations of one to several species of *Ambystoma*. By contrast, in the Pacific Northwest, larval *D. ensatus* occupy all of these aquatic environments, sharing seepages and small streams only with the diminutive larvae of *Rhyacotriton olympicus* and the lotic habitats with possibly two species of *Ambystoma*. Except for the closely related and largely allopatric *D. copei*, *D. ensatus* has no salamander competitors in the larger streams and rivers of the Northwest.

The concept of eurytopy in *D. ensatus* has significance in relation to an hypothesis proposed by Smith (1969). Smith recognized a correlation between eurytopy and cryptic speciation, and predicted that with close study, some of the wide-ranging, relatively eurytopic species of amphibians and reptiles would be resolved into series of two or more cryptic species. Such has proven to be the case with *D. ensatus*. Previous to 1970, the genus *Dicamptodon* was thought to be monotypic. However, Nussbaum (1970) showed that some populations in western Washington and extreme northwestern Oregon belonged to an undescribed species, *D. copei*, which differed from the nominate species, *D. ensatus*, only in details of morphology and life history. Hence Smith's criteria of eurytopy and cryptic speciation seem to be met in the case of *Dicamptodon*.

Summary

1. The structure of larval populations of *D. ensatus* varies greatly. Variation at least partly reflects differences in growth rates and time of year of metamorphosis. Population structure is determined largely by the nature of the aquatic environment.

2. In small streams, metamorphosis normally occurs in the second year of larval life; neotenes are rare.

3. In large streams, ponds, and lakes, neoteny is common; and neotenes likely constitute the major breeding force. Distinct age-classes of larvae are difficult to detect in these habitats, perhaps because of asynchronous oviposition by neotenes.

4. Larvae hatch at $\bar{x} = 18.25$ mm snout-vent length and $\bar{x} = 34.42$ mm total length, but remain prefeeding for another three to four months. Feeding begins at $\bar{x} = 24.43$ mm SVL and $\bar{x} = 47.24$ mm TL.

5. Growth rates of first-year larvae are known to vary from about 1.0 to 12.5 mm total length per month during the warm season.

6. The largest-known *D. ensatus* is a neotene which measures 205 mm SVL and 351 mm TL. This is apparently the longest-known ambystomatid and certainly the most massive.

7. Larvae may transform in natural populations at 92 to 166 mm TL (53 to 93 mm SVL).

8. *D. ensatus* is an eurytopic species. Larvae are found in a wider variety of aquatic habits than is generally believed. To classify the larvae as strictly mountain brook forms is inaccurate and misleading, morphological features notwithstanding. Eurytopy in larval *D. ensatus* may be partially a reflection of lack of salamander competitors across the range of aquatic environments in the Pacific Northwest.

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