Growth and food of larval *Ambystoma gracile* from a lowland population in southwestern British Columbia

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Growth and food of larval *Ambystoma gracile* from a lowland population in southwestern British Columbia were studied.

In late March the salamander larvae hatch at a snout–vent length of 8 mm. After 13 to 14 months, most larvae metamorphose at about 50 mm *s–v* length. A small percentage of the population is neotenous.

Food eaten by both small and large larvae is similar. A few prey items, especially small dipteran larvae and crustaceans, are eaten in abundance during all months and represent the bulk of most food taken by all size larvae.

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On a étudié la croissance et l'alimentation des larves d'*Ambystoma gracile* habitant une région de basses terres dans le sud-ouest de la Colombie Britannique.

Les larves de salamandres éclosent vers la fin de mars et leur longueur du museau à l'anus est de 8 mm. Après 13–14 mois, la plupart des larves se métamorphosent; leur longueur museau–anus est alors d'environ 50 mm. La néoténie n'existe que chez un petit pourcentage de la population.

Les petites et les grosses larves ont une alimentation semblable. Il se consomme en abondance, et pendant toute l'année, des proies peu variées, surtout des petites larves de diptères et des petits crustacés, qui constituent la plus grande partie de l'alimentation chez toutes les larves, quelle que soit leur taille.

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Introduction

Populations of the northwestern salamander, *Ambystoma gracile*, are found from sea level to 2500 m from southern British Columbia to northern California. Some studies have been directed to adult behavior, including breeding (Slater 1936; Licht 1969), defense (Brodie and Gibson 1969), vocalization (Licht 1973), and larval forms (Watney 1941; Snyder 1956; Efford and Mathias 1969). However, much of the information on larvae has come only from random collections made at different localities.

Growth rates of each stage are an important part of a species' life history strategy (Cole 1954; Gadgil and Bossert 1970), and growth rates of individuals from different populations may vary markedly. For example, Tilley (1973) found that high-altitude populations of the salamander *Desmognathus ochrophacus* showed different growth rates and achieved maturity later than lowland animals. Licht (1975) has shown the same for frogs.

In this report I present data on natural growth rates from egg to metamorphosis for *A. gracile* living at 70 m in southwestern British Columbia.

Also in this report is information on the food eaten by salamanders during larval life. Studying larval diet with growth not only allows one to learn about the kinds of prey taken but also to ascertain whether diet changes with age and size.

Study Area and Methods

Salamanders were collected from the Little Campbell River (LCR) about 5 mi from White Rock, British Columbia. At the collection site, the river is a permanent slow-moving stream with mud bottom and channel varying from 1 to 2 m deep in the centre to 0.2–0.5 m deep on the gradually sloping edges. Except during rain, there is little current. The stream flows through highly productive marsh habitat and *Carex*, *Potamogeton*, and *Typha* grow heavily along its course. From late November to late January the river may be frozen over. Water temperatures from March to November range from 7 to 30 °C in the shallows, and the main channel is usually 15–26 °C.

The rough-skinned newt, *Taricha granulosa*, and several anurans also inhabit the river environs.

From June 1968 to June 1969, during the 2nd week of each monthly, I collected larval *A. gracile*. Each monthly sample was collected around noontime on a single day. (The river was frozen over in January 1969 and no sample was collected for that month.) All animals were collected from the same 75-m stretch of river by use of a fine-mesh seine dragged along the mud bottom of the main river channel.

After collection, specimens were sacrificed and immediately preserved in 5% formalin. Later, measurements were made of snout–tail and snout–vent (*s–v*) lengths, and all animals were weighed to the nearest mg. Stomachs were removed and all contents weighed. All items were identified and classified to ordinal level, to family, or to genus if the item was particularly abundant and well-represented in the diet.

In the laboratory, larvae were kept in 10-gal aquaria, and live prey, such as small tadpoles, snails, and crustacea, were offered to them. I observed general feeding behavior and movements of hunting animals.

Results

Breeding and Egg Deposition

In the LCR study area, *A. gracile* breed in late March and early April when breeding sites are free from ice and the water is about 6–8 °C. Egg masses are firm and globular and 8–15 cm in diameter. Each mass is attached firmly to vegetation, with a sedge or bulrush stalk usually through the mass centre. Masses are laid about 0.5–1 m deep. Ova are light brown to cream-colored, and ovum diameter is 1.5–2.4 mm. Eight egg masses averaged 106 eggs (range of 74–126). A detailed description of the breeding behavior of *A. gracile* can be found elsewhere (Licht 1969).

In 1968, eggs laid the last week of March hatched about 4 weeks later.

Larval Growth

At hatching, 20 larvae taken directly from egg masses averaged 7.8 mm (range of 7.3–8.6) in snout–vent length.

The first collection of free-swimming larvae was made in the 2nd week of June, about 1 month after larvae hatched. Growth of larvae measured by snout–vent length and weight from hatching to near metamorphosis is shown in Fig. 1. The tail is about 50% of the total length of the animal so that each animal is about twice as long as the snout–vent measurement. Many individuals had tails with broken or regenerative tips, likely the result of near capture by fish or invertebrate predators.

Larvae caught in June had very small hind limbs if any at all. By July all four limbs were developed.

Total body weight was positively correlated with body length (Fig. 2). Most rapid growth occurred from June to September of the 1st year

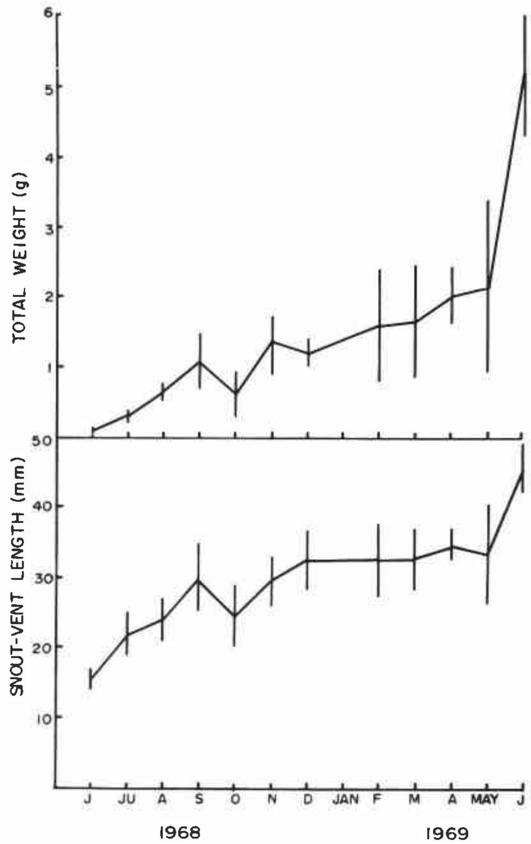

FIG. 1. Snout–vent length and weight. Growth of larval *Ambystoma gracile* from hatching to near metamorphosis. Points are means and vertical bars represent 95% confidence limits around means.

and again in May and June of the 2nd year. During these months water temperatures are high and feeding activity would be maximal. Very little growth seems to occur during cold months although the animals do remain active and can feed.

About 13–14 months post hatching, metamorphosis occurs. At this time animals are between 45–55 mm snout–vent length (90–110 total length). Seven newly transformed salamanders collected in late June under logs along the river margins averaged 52.1 mm *s–v* length (range of 46–58 mm). By July no 2nd-year larvae were found in the river.

An unknown, but small percentage of individuals in the LCR population remain neotenous, or permanently aquatic. Two adult females, 83 and 87 mm *s–v* length, with developed ovaries, were caught in March 1969.

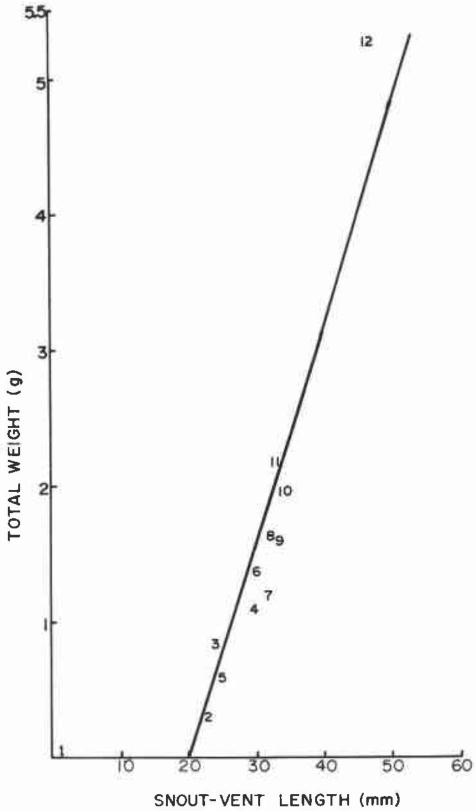

FIG. 2. Relationship of body length to body weight in larval *Ambystoma gracile*. Line is represented by $y = -3.3059 + 0.1623x$ ($r^2 = 85.6$), where y is total weight and x is snout–vent length. Points plotted are means of body length and body weight for each monthly sample, where 1 is June 1968, 2 is July, 3 is August, etc.

Food

The results of stomach content analysis for monthly collections of larvae are presented in Table 1.

No salamander larvae had an empty gut, even in winter, and none seemed in poor condition. Certain items are eaten during almost all months. Especially common are dipteran larvae, particularly the midges (Tendipedidae) and small crustaceans (Cladocera and Ostracoda).

There are 30 food classes in all samples combined, but 10 of these classes represent 89% of all food items. Table 2 shows the top 10 items and the percentage of items from all samples and from each monthly sample they comprise. Certain items deserve comment. Nematodes found in all samples, except June 1968, represent the second most abundant item. In February 1969, nematodes were 68% of all items. It is likely, however, nematodes are not food but rather parasites within salamanders. Because nematodes occupy space in the gut and thus reduce stomach capacity suitable for food, they have been listed with other food items found in stomachs.

Another questionable food item is *Potamogeton* seeds. Whether larvae get nourishment from such plant material is unknown. As visual predators, larvae probably grabbed moving seeds which fell into the water.

Larvae collected in winter (Nov.–Mar.) had food in stomachs. No larvae in any monthly sample had an empty gut. However, larvae collected in winter months showed fewer food classes than in other months, although salamander sample sizes in winter months are very low and may be partly responsible for this finding. Some feeding activity apparently occurs throughout winter.

Growth and Food

Salamanders of all sizes feed on virtually the same prey items. Although there are some quantitative differences, food of small larvae collected in 1968 is essentially the same as those eaten by larvae a year older. Data in Table 2 support these statements. Varying numbers of the top 10 items listed were found in each monthly sample, ranging from all 10 in July to only 4 of the 10 in March. However, in all samples, those of the 10 found represent from 75% to 96% of total items in that sample. In other words, these top 10 items are eaten very commonly and represent a major portion of the diet in all size larvae. The quantity of food eaten differs between larvae, with large larvae eating more food (Fig. 3), but larvae of different age and size tend to eat the same foods.

Food weight and total body weight are directly correlated (Fig. 3). Throughout the year, larvae average 6.2% (3–14%) of body weight as food. Highest food weights relative to body weights (10–14%) were found in larvae collected in March, April, and May of the 2nd year. However, this increased food weight of large larvae may be due in part to the presence of a few large items like large Plecoptera or Trichoptera nymphs which were inaccessible to small larvae. Large larvae ate the same kinds of food items as small individuals, but they ate more, as indicated by the linear correlation of Fig. 3.

TABLE 1

Food items as percentage by number in stomachs of *Ambystoma gracile*

Item	Jun.	July	Aug.	Sep.	Oct.	Nov.	Dec.	Feb.	Mar.	Apr.	May.	Jun.	Total sample
Nematoda	—	3.6	3.1	6.1	7.4	7.4	17.0	68	25.4	26.3	33.2	1.1	13.8
Annelida													
Oligochaeta	—	—	—	0.8	—	—	3.8	—	1.6	1.0	—	—	0.4
Hirudinea	—	—	—	3.0	—	—	—	—	1.6	—	0.5	—	0.5
Mollusca													
Planorbidae	8.2	1.8	0.9	11.4	1.0	—	—	—	—	—	8.1	63.7	6.1
Pelycopoda	—	0.6	1.8	1.5	—	—	—	—	4.8	0.5	3.3	5.5	1.2
Crustacea													
Cladocera	13.6	2.4	4.5	7.2	32.0	—	1.9	2	—	14.3	19.0	2.2	13.3
Ostracoda	16.9	5.5	—	—	14.8	37.0	13.3	10	11.1	9.1	—	—	7.8
Amphipoda	0.5	3.0	3.2	1.1	0.3	3.7	3.8	10	20.7	2.8	4.4	—	2.7
Anostraca	1.1	—	—	—	—	—	—	—	—	—	—	—	0.1
Isopoda	0.6	—	—	0.6	—	—	—	—	—	—	—	—	0.1
Copepoda	—	1.8	—	0.4	7.5	—	—	—	—	—	—	—	1.5
Arachnida													
Hydracarina	—	—	—	—	—	—	—	—	—	0.3	—	—	0.1
Insecta													
Ephemeroptera nymph	—	1.8	5.8	24.7	0.3	7.4	—	2	—	3.3	14.6	7.7	6.3
Trichoptera larvae	—	—	0.5	1.5	—	—	—	—	—	—	—	—	0.2
Trichoptera	0.5	—	—	—	1.3	—	—	—	—	0.3	—	—	0.3
Plecoptera	—	1.8	1.4	1.9	—	—	—	—	—	1.0	1.1	2.2	0.9
Coleoptera larvae	—	—	—	—	—	22.2	9.4	4	—	0.3	—	—	0.7
Coleoptera	—	1.8	1.0	0.4	1.1	—	—	—	—	—	2.1	1.1	0.7
Hemiptera nymph	—	10.3	—	—	—	—	—	—	—	—	—	—	0.8
Hemiptera	0.5	1.2	1.4	2.3	1.1	—	3.8	—	—	0.8	1.1	—	1.1
Neuroptera	—	—	—	0.8	—	—	—	—	—	—	—	—	0.1
Odonata	—	0.6	1.4	3.8	2.9	3.7	—	—	—	0.3	0.5	5.5	1.6
Diptera pupa	0.5	1.8	0.5	—	—	—	1.9	—	—	—	—	—	0.3
Diptera nymph	0.5	1.2	2.7	0.4	—	—	5.7	—	1.6	2.0	—	1.1	1.1
Diptera larvae													
Cyclorrhapha	26.6	17.6	—	0.8	6.2	—	—	—	—	—	1.6	7.7	5.5
Orthorrhapha													
Nemotocera	22.3	40.1	68.1	18.9	0.6	18.5	39.7	4	33.4	36.2	9.8	—	25.2
Brachycera	2.0	—	—	—	0.8	—	—	—	—	—	—	—	0.3
Potamogeton seeds	6.0	2.4	4.0	8.7	22.2	—	—	—	—	—	—	—	6.3
Plant tissue	—	—	0.5	4.2	0.3	—	—	—	—	0.8	0.5	1.1	0.9
Rocks	0.5	—	—	0.4	—	—	—	—	—	—	—	—	0.1
Total no. of food items examined	184	165	224	264	379	27	53	50	62	401	184	90	2083
No. of *A. gracile* examined	26	23	31	31	23	4	9	5	7	19	14	8	200

TABLE 2

The 10 most abundant food items found in stomachs of *A. gracile* from all monthly samples and the percentage each comprises of total items from each monthly sample

Item	% of all items from all samples	% of all items in monthly samples											
		Jun. (14)	Jul. (19)	Aug. (16)	Sep. (21)	Oct. (17)	Nov. (7)	Dec. (10)	Feb. (7)	Mar. (8)	Apr. (16)	May (14)	Jun. (11)
Nematocera	25.2	22.3	40.1	68.1	18.9	0.6	18.5	39.7	4	33.4	36.2	9.8	—
Nematoda	13.8	—	3.6	3.1	6.1	7.4	7.4	17.0	68	25.4	26.3	33.2	1.1
Cladocera	13.3	13.6	2.4	4.5	7.2	32.0	—	1.9	2	—	14.3	19.0	2.2
Ostracoda	7.8	16.9	5.5	—	—	14.8	37.0	13.3	10	11.1	9.1	—	—
Ephemeroptera	6.3	—	1.8	5.8	24.7	0.3	7.4	—	2	—	3.3	14.6	7.7
Potamogeton seeds	6.3	6.0	2.4	4.0	8.7	22.2	—	—	—	—	—	—	—
Planorbid snail	6.1	8.2	1.8	0.9	11.4	1.0	—	—	—	—	—	8.1	63.7
Cyclorrhapha	5.5	26.6	17.6	—	0.8	6.2	—	—	—	—	—	1.6	7.7
Amphipoda	2.7	0.5	3.0	3.2	1.1	0.3	3.7	3.8	10	20.7	2.8	4.4	—
Odonata	1.6	—	0.6	1.4	3.8	2.9	3.7	—	—	—	0.3	0.5	5.5
Total	88.6	94.1	78.8	91.0	82.7	87.7	77.7	75.7	96	90.6	92.3	91.2	87.9

NOTE: Figure after item is the percentage that particular item comprises of total items from all monthly samples. Figure in parentheses next to each month is the total number of food classes found in that monthly sample. Figure under each month is the percentage of all items in that sample that the particular food item comprises; —, indicating none found in sample.

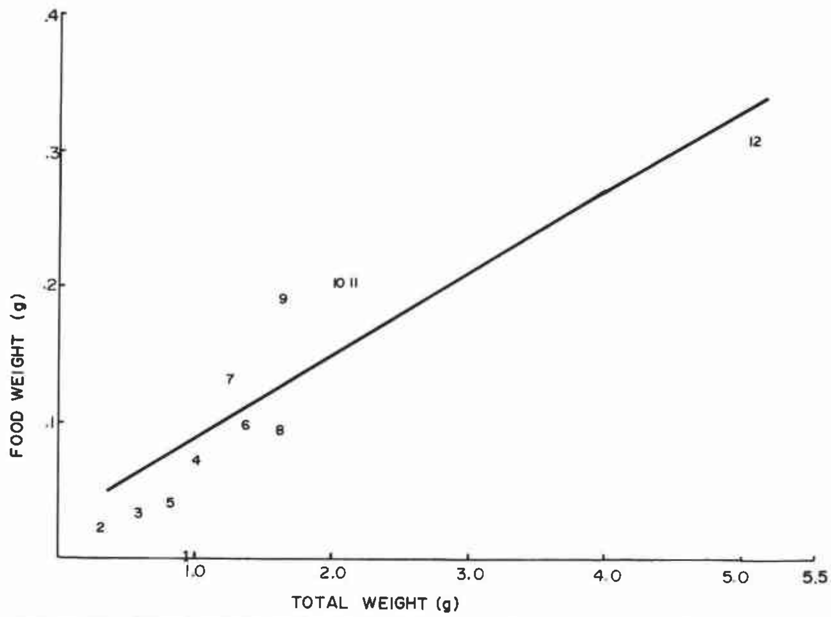

FIG. 3. Relationship of food weight and total weight in larval *Ambystoma gracile*. Line is represented by $y = 0.0295 + 0.0616x$ ($r^2 = 80.01$), where y is food weight and x is total weight. Points plotted are means of food weight and total weight for each monthly sample, where 1 is June 1968, 2 is July, 3 is August, etc.

Feeding Behavior

Laboratory observations made on larval *A. gracile* showed that small organisms which move slowly on the substrate are quickly caught. Salamanders will move to examine a stationary prey, but they will snap at it only if it moves. Visual cues seem most important for securing prey; however, fast-swimming prey like anuran tadpoles are not as readily caught as slow organisms like planorbid snails.

Discussion

After hatching most rapid growth of larval *A. gracile* occurs during the warmer months, between June and September of the 1st year and May and June of the second. Given the fact that some feeding takes place in winter months, growth may occur, but is too slow to be measured. Warmer water allows greater hunting activity and more prey will be available.

Prey items eaten are nearly the same for all larvae, although large larvae will take more large Trichoptera and Plecoptera, items too large for the newly hatched larvae. Anderson (1968) found the same in a study of larval *Ambystoma macrodactylum*, a salamander also found in western North America. In fact, these two *Ambystoma* overlap in range and given the similarity of their larval diet, a study of food habits where they are sympatric is warranted.

Because food availability was not studied it is not possible to determine if *A. gracile* show true food preferences. Hamilton (1940) studied larval newts (*Diemicthylus viridescens*) and concluded that they show no preference for food items but take what is accessible and available. However, Henderson (1973) showed that larval *A. gracile* can learn to select certain prey, so the possibility that preferences exist cannot be excluded.

A. gracile feed on the same items throughout larval life, and normally eat dipteran larvae, small crustaceans, and small molluscs. It is possible that these items are preferred and selected from others also available, but this cannot be stated with certainty. These items are most easily caught since they provide good visual cues and are slow moving. As well, these prey items are abundant (subjective assessment) in almost all samples of mud taken from the river.

A small percentage of larvae remains permanently aquatic. In Marion Lake, about 300 m in altitude near Haney, B.C., a larger portion of larvae is neotenous. Neish (1971) found a ratio of 50:50 in breeding adults and apparently the lake supports a relatively large neotenous population. High-altitude populations of *A. gracile* may show more neoteny and Sprules (1974) has recently discussed various hypotheses for this phenomenon.

The question as to whether *A. gracile* from different altitudes differ in larval growth rate and duration of larval life cannot be conclusively examined because no detailed study of high-altitude forms has been done. In Marion Lake at 300 m, *A. gracile* show signs of metamorphosis at 13–14 months as do LCR animals; as well they metamorphose at the same size, about 50 mm *s–v* length. Snyder (1956) collected *A. gracile* at various localities from above 1300 m on Mt. Rainier. He describes differences in coloration between low- and high-altitude forms, but he provides no details on size of 1st-year larvae. Snyder makes the assumption that montane *A. gracile* grow more slowly and also attain metamorphosis size at a later age, but no evidence supports his assumption.

The data presented here on lowland forms can be used for comparison with similar data collected in a systematic way from very high-elevation populations, and life history adaptations to altitude may be discovered.

Acknowledgments

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