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A COMPARISON OF THE FOOD HABITS OF *AMBYSTOMA MACRODACTYLUM SIGILLATUM*, *AMBYSTOMA MACRODACTYLUM CROCEUM*, AND *AMBYSTOMA TIGRINUM CALIFORNIENSE*

JAMES D. ANDERSON

Studies on the food habits of single species of salamanders in one area have generally indicated a lack of selectivity (Hamilton, 1940). Farner (1947) however demonstrated divergence of feeding habits between sympatric species, and Anderson and Martino (1967) reported intraspecific differences in different habitats. The latter authors stressed the importance of comparative studies of food habits within and between species. Salamanders of the genus *Ambystoma* are ideal for such comparative studies since adults frequently live under diverse environmental conditions and since the larvae of two or more species often share the limited resources of pond ecosystems. The present study compares the food habits of the following: 1) adult and larval *Ambystoma macrodactylum croceum* and *A. m. sigillatum*; 2) sympatric larvae of *A. m. croceum* and *A. tigrinum californiense*; 3) different age classes of one population of *A. m. sigillatum*.

Ambystoma macrodactylum is widely distributed throughout western North America in many diverse habitats. The subspecies *croceum* is restricted to a few ponds near sea level in Santa Cruz County, California, and in one pond the larvae live sympatrically with *Ambystoma tigrinum californiense*. In this region both species have a simple, short larval period of about 4 months. *Ambystoma macrodactylum sigillatum* occurs from southern Oregon south in the Sierra Nevada to Tuolumne County, California. At high elevations the larval period is about 14 months and the larvae of one year coexist for several months with those of the succeeding year.

The study ponds and habitats were described in detail by Russell and Anderson (1956) and Anderson (1967). The life history, growth, and habits of larval and adult *A. m. croceum* and *A. m. sigillatum* were described by Anderson (1967), thermal histories of both populations by Anderson (1968), and the taxonomy and relationships of the populations by Russell and Anderson (1956) and Ferguson (1961). The life history and habits of *A. tigrinum californiense* were discussed by Storer (1925) and Stebbins (1951).

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The diet of adult *Ambystoma macrodactylum* was discussed by Schonberger (1944) and Farner (1947), both of whom studied the isolated population of *A. m. sigillatum* at Crater Lake, Oregon. There are no published accounts of the feeding habits of larval *A. macrodactylum*. Dineen (1955) and Burger (1950) described certain aspects of feeding in *A. t. tigrinum*, but there are no reports on the feeding habits of *A. t. californiense*.

Materials and Methods

Adults and larvae collected for stomach analysis were killed and preserved in 10% formalin in the field. Notes were taken on the relative abundance of the fauna where the salamanders were collected. Later specimens were measured (snout-vent and total length), and the stomachs removed and examined for food. The food items were identified and counted for all specimens; food items were also weighed. Excess fluid was removed and a crude wet weight taken. Weights were taken only of whole food items and adjusted for fragmented items. For small items (e.g., copepods and cladocerans) 50 or 100 individuals were weighed and an average weight obtained for individuals.

For adults the items were analyzed as per cent frequency (number of stomachs containing the item/total number of stomachs). Food items for larvae were similarly analyzed, but in addition the total weight of each item was calculated and the percentage by weight (total weight of item/total weight of all food items) determined.

The samples of larval *A. m. croceum* and *A. t. californiense* were taken on the same days between 10 AM and noon. All were collected in Ellicott Pond (Santa Cruz County, California) during March, April and May 1958. Larval *A. m. sigillatum* were collected between 10 AM and noon from a single pond near Mosquito Lakes, 8050 feet, Alpine County, California. Samples of age classes compared were also taken on the same days.

Adults of both subspecies were collected whenever available. The samples of adult *A. m. croceum* were taken from March through November at Ellicott Pond, Santa Cruz County, California. Those of *A. m. sigillatum* were taken at Mosquito Lakes, Alpine County, during May and June, in or near the breeding ponds. The adults of *sigillatum* are abundant on the surface only during the breeding season (Anderson, 1967).

Results

Adults.—As is true for most terrestrial salamanders, arthropods make up the bulk of the diet in adults of *A. m. croceum* (Table 1) and *A. m. sigillatum* (Table 2). Isopods are the most important

TABLE 1.—Stomach contents of 38 adult *Ambystoma macrodactylum croceum*.

Item	No. of stomachs containing item	No. of items	Per cent of stomachs containing item	Per cent of total number of items
Cast skin	8	8	21.1	10.4
Annelida				
Lumbricus	4	5	10.5	6.5
Mollusca				
snail	1	1	2.6	1.3
slug	5	5	13.2	6.5
Arthropoda				
Chilopoda	3	3	7.9	3.9
Isopoda	19	36	50.0	46.8
Araneida	1	1	2.6	1.3
Insecta				
Collembola	1	1	2.6	2.6
Lepidoptera	1	1	2.6	2.6
Diptera	1	1	2.6	2.6
Orthoptera				
Blattidae	1	1	2.6	2.6
Gryllidae	3	3	7.9	3.9
Coleoptera				
Carabidae	6	7	15.8	9.1
Staphylinidae	2	2	5.3	2.5
Elateridae	1	1	2.6	1.3
Curculionidae	1	1	2.6	1.3
Unidentified	1	1	2.6	1.3

prey of *A. m. croceum* all through the year, but especially in the drier months.

The fauna available to *A. m. croceum* during the summer dry season consists of isopods, slugs, crickets, ants, ear-wigs, and juvenile *Hyla regilla*. *Ambystoma m. croceum* is not known to eat the last three items, although they are fairly numerous and of suitable size. A few salamanders ate slugs and crickets; however, the major portion of their diet consisted of isopods, which were found in all stomachs examined. Isopods are always readily available to *A. m. croceum*, not only because they are numerous, but also because they aggregate in the same moist places as the salamanders.

During the wetter months of the year, the fauna under logs is more abundant, and isopods, beetles, centipedes, earthworms, and spiders are important food items for *croceum*. However, isopods are taken less frequently during this season than in the summer.

The diet of *A. m. sigillatum*, in contrast to that of *croceum*, consists almost entirely of spiders and insects rather than isopods. Aquatic dipterans (mosquitoes and tendipedids) were taken from the stomachs of males found in the breeding ponds; the stomachs of females from the ponds were either empty or contained only terrestrial insects. This reflects behavioral differences between the sexes:

TABLE 2.—Stomach contents of 20 adult *Ambystoma macrodactylum sigillatum.*

Item	No. of stomachs containing item	No. of items	Per cent of stomachs containing item	Per cent of total number of items
Cast skin	3	3	17.6	2.1
Arthropoda				
Isopoda	1	1	5.9	0.7
Araneida	4	15	23.5	10.4
Insecta				
Collembola	1	15	5.9	10.4
Diptera				
Mosquitoes				
Adults	1	6	5.9	4.2
Pupae	3	73	17.6	50.7
Chironomidae	2	3	11.8	2.1
Orthoptera				
Tettigonidae	3	4	17.6	2.8
Unidentified	1	1	5.9	0.7
Coleoptera				
Carabidae				
Adults	2	5	11.8	3.5
Larvae	1	1	5.9	0.7
Staphylinidae	4	5	23.5	3.5
Curculionidae	1	1	5.9	0.7
Tenebrionidae	1	1	5.9	0.7
Buprestidae	2	3	11.8	2.1
Elateridae	1	1	5.9	0.7
Unidentified	3	6	17.6	4.2

the females enter the water, mate, deposit eggs, and leave within a short time; males remain in the ponds for the entire breeding season.

Larvae.—The same food items are eaten by larval *A. m. croceum* and *A. tigrinum californiense*, but are of different relative importance to the species (Table 3, Fig. 1). The frequency of small crustaceans (cladocerans, copepods and ostracods) is high in both species but percentages of the other major items—tendipedids, snails, and tadpoles—differ significantly. Tendipedid larvae are most important to *A. m. croceum*, but tadpoles, and to a lesser extent snails, are preferred by *tigrinum.* When analyzed by weight the divergence in feeding habits is more conspicuous (Fig. 2). Tadpoles are clearly the dominant item taken by *tigrinum*, whereas four items constitute the bulk of the diet of *croceum.*

Two factors in the weight analysis require explanation: (1) the high per cent by weight of oligochaetes for *croceum* is based on a single large worm eaten by one larva and is therefore not as significant as indicated in Fig. 2; (2) the per cent weight of tadpoles for *croceum* is probably too high since the calculations are based on the size of tadpoles eaten by *tigrinum.* Almost every tadpole found

TABLE 3.—Stomach contents of 26 larval *Ambystoma macrodactylum croceum* and 32 *Ambystoma tigrinum californiense*.

Item	Number of stomachs containing item	Total no. of item	Per cent of stomachs containing item	Average weight (g)	Total weight	Per cent by weight
A. tigrinum:						
Cladocera	30	1400	93.7	.0005	.07	0.63
Copepoda	18	80	56.2	.0005	.004	0.04
Ostracoda	5	9	15.6	.010	.09	0.80
Amphipoda	1	4	3.1	.004	.02	0.18
Chironomidae	6	39	18.7	.005	.195	1.74
Chaoborus	1	1	3.1	.004	.004	0.04
Corixidae	5	7	15.6	.006	.042	0.37
Snails	13	27	40.6	.030	.81	7.17
Tadpoles	22	67	68.7	.150	10.05	89.03
A. m. croceum:						
Cladocera	21	620	80.8	.0005	.03	1.12
Copepoda	16	121	61.5	.0005	.006	0.22
Ostracoda	6	34	23.1	.010	.340	12.64
Chironomidae	14	128	53.8	.005	.640	23.79
Chaoborus	3	3	11.5	.004	.012	0.45
Corixidae	4	7	15.4	.006	.042	1.56
Coleoptera	1	1	3.8	—	—	—
Snails	3	5	11.5	.030	.150	5.58
Leeches	1	1	3.8	.120	.120	4.46
Oligochaeta	1	1	3.8	.600	.600	22.30
Tadpoles	6	6	23.1	.150	.750	27.88

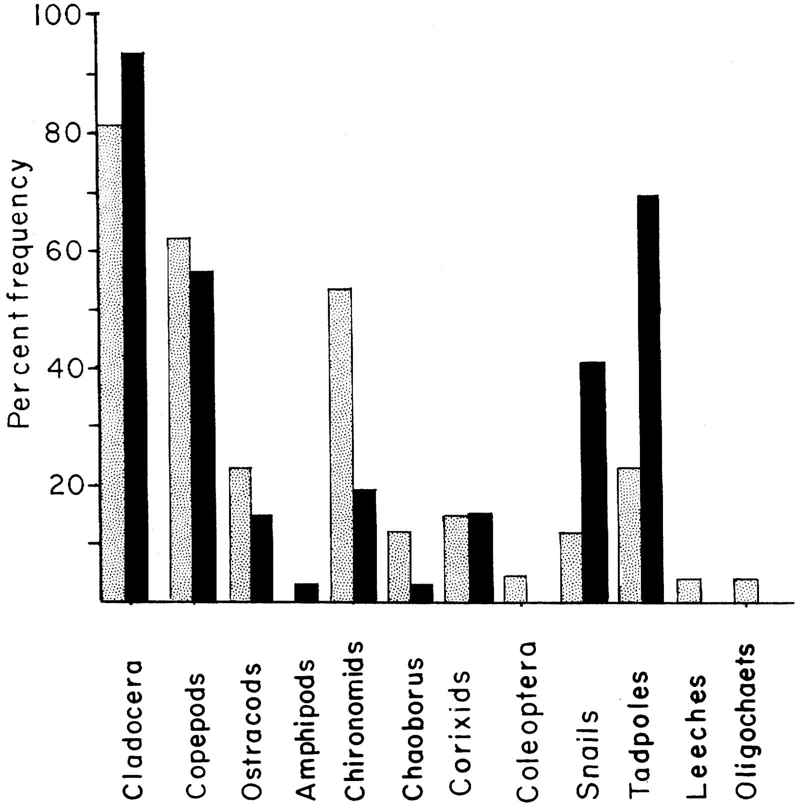

FIG. 1.—Per cent frequency of prey items of 26 larval *Ambystoma macrodactylum croceum* (stippled) and 32 larval *Ambystoma tigrinum californiense* (solid).

in *tigrinum* was intact, but the majority of those in *croceum* were fragmentary. The smaller *croceum* larvae apparently are unable to swallow whole tadpoles and probably attack and fragment smaller ones. Thus the difference between the species in bulk of tadpoles eaten is almost certainly greater than indicated.

Small larvae of both species feed mainly on cladocerans and copepods, both of which are extremely abundant in the pond. However, larval *A. tigrinum* grow more rapidly than *A. m. croceum*, and within 2 weeks the salamanders differ significantly in size; paralleling this is the observed divergence in feeding habits, in which *tigrinum* preferentially selects tadpoles (mostly *Hyla regilla* but a few *Rana aurora*), and *croceum* selects tendipedids as the staple.

For gross comparison with the *Ambystoma* from Santa Cruz County the food items for all 60 larval *A. m. sigillatum* are presented in Table 4. As was true of the other populations, copepods and cla-

TABLE 4.—Stomach contents of 60 larval *Ambystoma macrodactylum sigillatum.*

Item	No. of stomachs containing item	No. of items	Per cent of stomachs containing item	Per cent of total number of items
Mollusca				
Pisidium	12	42	20.0	2.7
Arthropoda				
Cladocera	42	563	70.0	36.7
Copepoda	35	319	58.3	20.8
Ostracoda	34	176	56.7	11.5
Eubranchiopoda				
Streptocephalus	1	1	1.7	0.07
Hydracarina	2	6	3.3	0.4
Insecta				
Diptera				
Chironomidae	51	275	85.0	17.9
Mosquitoes				
larvae	17	78	28.3	5.1
Chaoborus	2	3	3.3	0.2
Coleoptera				
Adult fragments	5	5	8.3	0.3
larvae	13	27	21.7	1.8
Tricoptera				
larvae	4	5	6.7	0.3
Unidentified	2	2	3.3	0.14

docerans occur with a high frequency. Ostracods are taken more frequently by larval *A. m. sigillatum* (56.7% frequency compared with 23.1% for *croceum* and 15.6% for *tigrinum*), and tendipedid larvae, an important item for *croceum*, are taken with an even greater frequency by *A. m. sigillatum* (85% compared with 53.8%). Mosquito larvae and pupae and the clam *Pisidium* were taken by a significant number of *sigillatum*, but did not occur in stomachs of *tigrinum* or *croceum*.

In the following paragraphs the data are analyzed to compare the age classes of *sigillatum* through the 1958 season. On 2 July 1958 only larvae that had overwintered (1957 group) were present in the pond. On 6 August and 20 August both age classes were present and actively feeding, but by 23 September the 1957 group had metamorphosed (see Anderson, 1967 for details of life history and overlap of age classes).

Table 5 compares the age classes present during the 1958 growing season and indicates the seasonal changes within each class. Both groups contain tendipedids in high frequency, but otherwise the small (1958) larvae show a high frequency of small items (cladocerans and copepods) and a low frequency of large (Tricoptera, Coleoptera, *Pisidium*) or agile (mosquito larvae) items. The influence of size is best illustrated by the Tricoptera larvae and the clams (*Pisidium*). Caddis-fly larvae were abundant and ac-

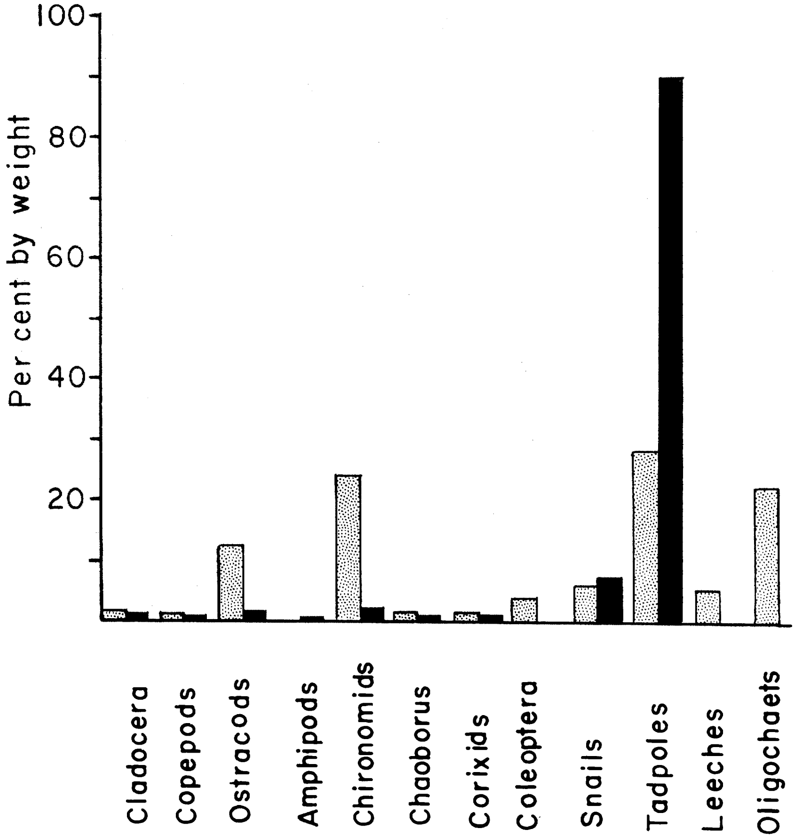

FIG. 2.—Food items of 26 larval *Ambystoma macrodactylum croceum* (stippled) and 32 larval *Ambystoma tigrinum californiense* (solid) compared by weight.

tive in the pond through the summer, but only large *sigillatum* larvae (1957 class) had eaten them. Presumably the tough cases of sticks and pine needles inhibited smaller salamanders, since in the laboratory small *Ambystoma* from many localities readily ate caddis-fly larvae removed from their cases. Clams were taken only by the largest 1958 larvae and by the two samples of larger 1957 larvae.

In addition to the size factor, availability is important, as shown by the occurrence of mosquito larvae. During early summer (June to late July) mosquito larvae and pupae are extremely abundant, but decrease and almost disappear in late July and early August. From mid-August through September they increase in abundance once more, apparently from a second breeding. On 2 July mosquitoes occur in all stomachs, but are absent from both age classes on 6

TABLE 5.—Per cent frequency of prey items in stomachs of two age classes of larval *Ambystoma macrodactylum sigillatum.*

Item	1957 Class (n = 30)	1958 Class (n = 30)	1957 Class (n = 10) July 2	Aug. 6	Aug. 20	1958 Class (n = 10) Aug. 6	Aug. 20	Sept. 23
Pisidium	30	10	0	50	40	0	0	30
Cladocera	50	90	10	80	10	70	100	100
Copepoda	30	87	30	50	10	60	100	100
Ostracoda	53	60	90	40	30	20	80	80
Streptocephalus	3	0	0	10	0	0	0	0
Hydracarina	0	7	0	0	0	0	10	10
Chironomidae	80	90	100	90	50	70	100	100
Mosquito Larvae	40	17	100	0	20	0	20	30
Chaoborus	3	3	0	10	0	0	10	10
Coleoptera								
Adults	7	10	10	10	0	0	0	30
Larvae	30	13	0	70	20	0	10	30
Tricoptera Larvae	17	0	10	30	10	0	0	0
Insecta (unidentified)	0	7	0	0	0	0	0	20

August. They again occur (20% frequency) in both groups on 26 August and in 30% of the 1958 group in September.

Notes on feeding behavior.—In the laboratory, adults of both subspecies of *Ambystoma macrodactylum* used olfactory and visual cues in obtaining prey. Quiescent adults were frequently stimulated to search for food by the odor of earthworms, isopods, and crickets out of their visual field. After the prey was located they did not attack until the object moved.

Larvae may also use olfactory cues, but seem to rely mostly on visual stimuli. Feeding behavior, which varies with size and stage of development, was observed in the field and the lab. Prior to the development of functional forelimbs and while the balancers are intact (roughly equivalent to Harrison stages 40–45), the larvae swim very little and feed only on objects passing directly in front of them. This "watchful waiting" method continues until all four limbs are functional, but the larvae make short lunges or dashes at moving items more frequently as their powers of locomotion increase. The lunges seldom exceed one body length. When the hind limbs are functional the larvae actively stalk prey. They crawl slowly toward a moving object and attack by a sudden dash of one to two body lengths. Little chewing is done, the teeth being used to hold the prey and position it for swallowing. Most feeding is done on the bottom, but large larvae swim toward the surface to capture moving items. Smaller larvae prefer to feed in a tangle of vegetation, but older larvae forage most often in the open.

Discussion

Farner (1947) studied the food habits of adult *A. macrodactylum* at Crater Lake, Oregon, and reported that it was a scavenger, feeding on dead aquatic insects and crustaceans. However adults of *A. m. croceum* and *A. m. sigillatum* show no indication of scavenging habits. Although some fragments were found in stomachs, most items appeared to be fresh, intact organisms. Moreover feeding behavior in the laboratory indicated the need for movement by the prey to elicit feeding reactions. The scavenging habit might be a special adaptation at Crater Lake for the avoidance of competition with *Taricha granulosa mazamae*, or for the lake-side habitat of the adult *Ambystoma*.

The difference in food habits between adults of *A. m. croceum* and *A. m. sigillatum* reflects the differences in their habitats. Geographic variation in food habits probably parallels their geographic variation in color, morphology (Ferguson, 1961) and life history (Anderson, 1967), all of which are adaptive to habitat differences and general climatic regimes.

The food habits of adult *A. tigrinum californiense*, sympatric with *A. m. croceum* in Santa Cruz County, California, were not studied. However, the great difference in size and non-breeding habitats makes it unlikely that there is overlap in food requirements.

Smallwood (1928) indicated that *Ambystoma maculatum* does not feed during breeding migration and the aquatic mating period in early spring. It has been assumed that similar species which emerge from hibernation at the first thaw and migrate immediately to breeding ponds behave in a similar fashion. The spring ritual of *A. m. sigillatum* is similar to that of *A. maculatum* (Anderson, 1967) but the feeding behavior is different. Male *A. m. sigillatum*, like males of many other species of salamanders that breed in the water, remain in the ponds for the duration of the breeding season. The presence of aquatic dipteran larvae in the stomachs of these salamanders indicates that they feed in the ponds during that period. The absence of food in stomachs of female *A. m. sigillatum* suggests that they do not begin feeding until after eggs have been deposited.

The differences in food habits of larval *A. m. croceum* and *A. m. sigillatum* are more complex than those of the adults. The ponds in Santa Cruz County are warmer, shallower, more productive and more diverse in species than those at high elevations in the Sierra Nevada. With the exception of mosquito larvae, all items occurred in greater densities on the coast. The Santa Cruz ponds become choked with vegetation soon after they fill, but the Sierran ponds develop very little vegetation. Thus bottom-dwelling forms like *Pisidium* are available to larval *A. m. sigillatum* but probably unavailable to larval *A. m. croceum* because of bottom vegetation. Conversely, tadpoles may easily escape larval *A. m. sigillatum* in the open water of the Sierran ponds; their restricted movements in the coastal ponds may make them more vulnerable to larval salamanders. Most of the differences in feeding can therefore be attributed to such habitat factors as cover and productivity, although divergence of feeding habits due to competition (inter- or intraspecific) is an important factor. Size and aggressiveness are additional factors determining food habits. The larvae of *A. tigrinum* are large and aggressive and attack disproportionately large prey items such as large tadpoles and snails.

The sympatric larvae of *A. t. californiense* and *A. m. croceum* apparently draw on similar food resources for about the first week of feeding activity, both species being adapted to the bloom of planktonic forms that occurs in late winter. The food habits quickly diverge, however, primarily because of the more rapid rate of development in *tigrinum*. After two weeks larval *A. m. croceum*, which continue to depend on several smaller prey items or staples, are outdistanced by the larger and more aggressive larval *tigrinum*, which feed almost entirely upon tadpoles, the largest food items available to them. Competition is greatly lessened by the divergence of feeding habits and may be further reduced by habitat or behavioral differences not detected by the methods employed in this study.

The larvae of *A. m. sigillatum* overwinter, and overlap most of the next growing season with larvae hatching the following year (Anderson, 1967). Burger (1950) presented evidence that a similar life history pattern in *A. tigrinum nebulosum* at high elevations in the Rocky Mountains resulted in cannibalism and the regular elimination of the younger age class. Such a peculiar trophic relationship is worthy of re-investigation. Although it may be true for *tigrinum* in special circumstances, it does not hold true for *A. macrodactylum* even in the limited pond ecosystems at high elevations. The differences in feeding habits of the two age classes are clearly indicated in Table 5. The differences are at least as distinct as those between *A. tigrinum* and *A. m. croceum* in coastal ponds. Although large larvae of *A. m. sigillatum* readily feed on smaller larvae in the laboratory or while being transported to the laboratory, no examples of cannibalism were detected in the field samples. Moreover, the habits and habitat selection of the two age classes are so different as to make contact and subsequent cannibalism unlikely (Anderson, 1967).

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Department of Zoology, Rutgers University, Newark, New Jersey 07102