Comparison of Size, Structure, and Distributional Patterns of Two Salamander Populations in Marion Lake, British Columbia[1]

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During 1968 and 1969, populations of *Taricha granulosa* and neotenous *Ambystoma gracile* were trapped and observed in Marion Lake, B.C. The adult *T. granulosa* and *A. gracile* populations were estimated respectively at 2450 and 14,500. It was estimated that there were about 45,000 *A. gracile* young of the 2nd year in the lake. These populations represent total lake biomasses of about 18 kg for *Taricha* and 408 kg for *Ambystoma.* The numbers of young larvae were not determined for either species. The *A. gracile* population was widely dispersed throughout the spring and summer. Density and size composition varied between areas with different vegetation and substratum. The *T. granulosa* distribution within the lake was highly contagious and changed through time. Although displaced animals returned to the areas where they were caught, the positions of their home ranges changed through time. *Taricha granulosa* entered the lake in April and May, showed evidence of wandering in midsummer, and left the lake in September and October. Fifty percent of adult *A. gracile* seen during the breeding season were metamorphosed and were found in the lake only during April and May. Neotenous adults remained in the lake all year, as did larvae of the 1st and 2nd years. Those larvae that metamorphosed did so in late August and early September. *Ambystoma gracile* grew rapidly in the lake, but no growth was seen in *T. granulosa.* No source of *T. granulosa* mortality was found in the lake, but *A. gracile* were preyed on by fish and diving bugs, and dead specimens were found on the lake bottom.

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MARION Lake, British Columbia, contains four predacious aquatic vertebrates. Two of these are salmonid fish, the rainbow trout (*Salmo gairdneri* (Richardson)) and the kokanee (*Oncorhynchus nerka* (Walbaum)). The other two are salamanders. One of these is the newt (*Taricha granulosa* (Skilton)) and the other is a neotenous form of *Ambystoma gracile gracile* (Baird). The larvae of both species also occur in the lake. As part of a continuing study on energy flow in Marion Lake, an intensive study is being made of predation by fish and salamanders.

An accurate assessment of the population structure and movements of both salamanders was necessary before their impact as predators could be established. Efford and Mathias (1969) have published the results of a study on this subject. The present paper describes the results of a continuation of their study.

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Methods

THE STUDY AREA

Marion Lake is a small mud-bottomed lake situated 10 km north of Haney, B.C. It is about 10 ha in area during the dry summer season, when most of the present work was done. The lake is situated at about 300-m elevation in a north–south valley heavily wooded with secondary coniferous forest. For a detailed description of the lake see Efford (1967).

A substratum map of the lake was made during a diving survey (Fig. 1). Seven substratum types were defined in terms of water depth and vegetation type.

"Open mud" areas of four water depths had a substratum of sediment containing sticks and leaves. During the summer a sparse cover of filamentous algae occurred in open mud areas deeper than 1 m. Shallower areas were covered with a thick mat of algae.

The substratum type referred to as "submerged vegetation" included areas having a growth of *Potamogeton epihydrus* (Raf.), *Chara globularis* (Thuill), and *Isotes occidentalis* (Henders.). These plants formed a mat on the lake bottom.

Potamogeton natans (L.) and *Equisetum* sp. are species of emergent plants that often occurred together, so areas containing these species were considered as one substratum type.

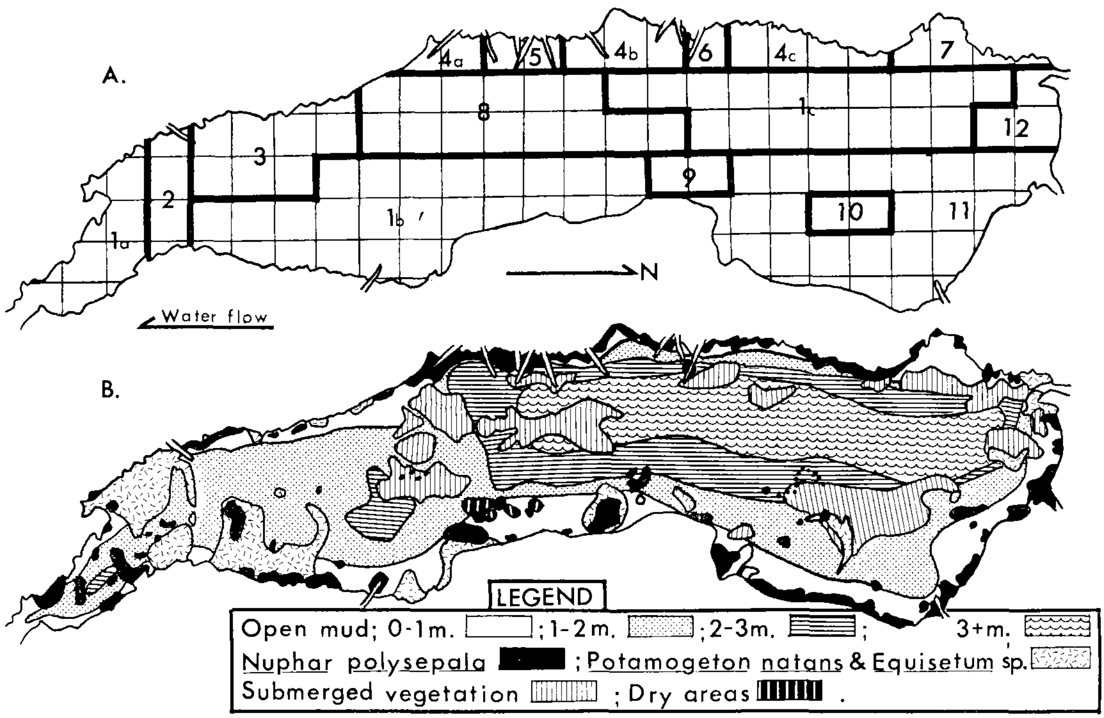

FIG. 1. Marion Lake: (A) the grid system shown was marked in the lake by means of numbered floats at the intersection of transects. The areas enclosed in heavy lines are referred to in Fig. 4 in the text; (B) substratum types, defined in terms of vegetation and water depth.

The largest emergent macrophyte in Marion Lake was the lily pad *Nuphar polysepala* (Engelm.). These plants grew in widely spaced clumps with open mud between them. In some instances *P. natans* grew among *N. polysepala*.

In Marion Lake the sizes and shapes of *P. natans*, *I. occidentalis*, *N. polysepala*, and *Equisetum* sp. beds changed from year to year. This can be clearly seen if Fig. 1 in this paper (showing 1969 data) is compared with Davies' 1966 data (Davies 1970).

Trapping and Observation

During the months of July–October 1968, and April–October 1969, *T. granulosa* and *A. gracile* were observed by the following methods:

(*a*) A set of floodlights was mounted on the stern of a rowboat. At night when the lake surface was calm both species of salamander could be seen in water not deeper than 3 m. From the boat *Taricha* could be captured with a dipnet. *Ambystoma* were able to escape the dipnet except when the water was colder than 10 C. This species was usually caught using a "slurp gun," which is a syringe-like device about 1 m in length with a spring-loaded plunger. During the 1969 study period the portion of the lake less than 3 m in depth was surveyed from a boat once per week.

(*b*) During July, August, and September 1968, 75 wire mesh funnel traps were distributed around the lake and were checked every 2 days. In 1969, funnel traps were placed in the lake according to a grid pattern (Fig. 1). The grid consisted of 114 traps placed at the corners of 1000-m² quadrats. Auxiliary traps were placed along the shoreline, giving a total of 132 traps. These were all checked five times per week during the period May 1–September 15 and twice per week until mid-October. The trapping program was discontinued at this time because few *Ambystoma* and no *Taricha* were being caught.

(*c*) Once per week from May 1 to September 15, 1969, the entire lake was surveyed with the use of skin-diving and scuba diving gear. *Ambystoma* could not be easily captured by a diver, but many *Taricha* were caught by hand.

Marking

All *Taricha* captured by the above methods were marked with individual toe clips. Immediately after capture the snout–vent measurement of each animal was recorded, its sex was determined, and if the animal was caught for the first time it was marked. The animal was then released at the site of capture, usually within a few minutes of being removed from the water.

Individual marking of *A. gracile* was done only during the summer of 1968. The regenerative powers of larval and neotenous *Ambystoma* were such that toe clips could not be used. It was therefore decided to loop color-coded threads around the gill rakers. This was done to 504 animals in the lake. Laboratory animals marked in this way did not lose their marks, but the method was so time consuming and the returns were so low (16 recaptures) that this program was not continued in 1969. All *A. gracile* captured in grid traps were measured and the *Ambystoma* catch record of each trap was kept. The sex of neotenous *A. gracile* could not be accurately determined.

Population Estimates

The size of the *Taricha* population was determined using the mark-recapture results of 1969. The estimate was calculated using the Schumacher modification of the Schnabel estimator (Ricker 1958, equation 18, p. 101). In view of the difficulty encountered in marking *Ambystoma*, it was decided to estimate the size of the *A. gracile* population using the following method:

(*a*) All *A. gracile* caught in the Marion Lake trap grid were counted and (after June 16) their snout-vent lengths were measured.

(*b*) All *A. gracile* were removed by trapping from three 9-m² plywood pens situated in Marion Lake. Known numbers of animals were then placed in these pens and were allowed to settle down for about 2 weeks.

(*c*) On 10 nights during July and August 1969 a glass-bottomed boat was rowed along grid transects in the 1–2 m deep open-mud portion of the lake, which occupied 21% of the lake bottom. The transects were 1 m wide and had a mean length of 275 m. The total number of *A. gracile* seen per transect was recorded. On the nights when transects were run, records were made of the number of animals that could be seen in the plywood enclosures. This allowed a calculation of the percent *A. gracile* exposed at the time of sampling.

(*d*) The number of *A. gracile*/m² on the transects was calculated as follows:

$$D = \frac{N \times 100/P}{A} \tag{1}$$

where D = density; N = number of animals seen on transect; P = percentage of animals observed in enclosures; and A = area of transect.

Correcting factors were employed to determine the density of *A. gracile* in subhabitats other than 1–2 m open mud. These factors were obtained as follows:

$$C = \frac{N_x}{N_m} \tag{2}$$

where C = the correcting factor; N_x = the mean number of animals per trap in subhabitat *x* (Table 1); N_m = the mean number of animals per trap in the 1–2 m open-mud part of the lake.

It was assumed that the catchability of *A. gracile* did not vary between subhabitats.

The number of animals in each subhabitat could be determined by the following expression:

$$N_y = D \times C \times A_y \tag{3}$$

where N_y = the estimated number of *A. gracile* in subhabitat *y*; D = estimated density of animals 1–2 m

Table 1. *Ambystoma gracile* population size data for neotenous adults and young of the 2nd year. The data were collected over 79 trapping days between June 3 and September 19, 1969. The mean percentage of animals hunting on a given night was 35.8% (range 21.0–52.4%). The mean number of animals seen on a transect through 1–2 m open mud was 0.425/m².

	Lily pads	*Potamogeton natans* & *Equisetum* sp.	Submerged vegetation 0–2 m deep	Submerged vegetation 2+ m deep	Open mud (*m*) 0–1	Open mud (*m*) 1–2	Open mud (*m*) 2–3	Open mud (*m*) 3+	Entire lake
No. animals caught	618	216	204	63	203	239	106	116	1762
No. traps	23	10	10	8	12	25	13	13	114
Mean no./trap	26.9	21.6	20.1	7.9	16.9	9.6	8.2	6.4	15.5
±1 SE	10.8	7.4	6.1	4.5	8.0	6.3	4.2	3.7	
Correcting factor	2.79	2.25	2.09	0.82	1.76	1.00	0.85	0.67	1.61
Area of substratum (*m²*)	5,481	9,795	7,020	5,290	17,190	30,245	15,015	19,800	109,836
A. gracile/m²	1.19	0.96	0.89	0.35	0.75	0.43	0.36	0.29	0.56
Total no. *A. gracile*	6,500	9,364	6,234	1,846	12,858	12,854	5,420	5,643	60,719
Mean wt *A. gracile* (*g*)	6.5	7.1	6.7	6.7	6.1	6.6	7.2	7.2	6.7
Estimated biomass/m² (*g*)	7.7	6.8	6.0	2.4	4.6	2.8	2.6	2.1	3.7
Total biomass (*kg*)	42.3	67.0	42.1	12.5	79.0	85.6	38.9	41.4	408.5
% lake area	5.0	8.9	6.4	4.8	15.7	27.5	13.7	18.0	
% biomass	10.3	16.4	10.3	1.2	19.3	21.0	9.5	10.1	

mud; C = correcting factor; A_y = area of subhabitat y.

The total of these figures gives an indication of the total lake population, excluding young-of-the-year, which were not caught in funnel traps and were not seen on the transects. The only animals included in the estimate are larvae in their second summer and neotenous adults.

(*e*) Over the 1969 trapping period the mean number of *A. gracile* per trap was calculated for each substratum type.

Results

Ambystoma gracile Population

The calculated *A. gracile* population approximated 14,500 adults and 45,000 young of the 2nd year (Table 1, Fig. 2). This represents a total midsummer biomass of 408 kg.

Size class distribution

The size frequency distributions of *A. gracile* for various periods and areas revealed three main size classes within the population (Fig. 2).

Young-of-the-year — These animals were about 0.9 cm long when they hatched during May and June. Larvae were not recruited into the trapped population until September probably because of their small size and their tendency not to move around until their legs are fully developed at 2.5–3.5 cm.

In May 1970, during a *Rana aurora* egg count, an attempt was made to count *A. gracile* eggs. It was found that *Ambystoma* eggs were often difficult to see, but about 750 egg masses were discovered. Egg masses were found in all quadrats of the lake. Lindsey (1966) found that the mean number of eggs in 22 egg masses was 47.4. Reckoned on this basis, at least 35,000 larvae of *Ambystoma* entered the population in 1970, but this may be an underestimate since many egg masses were probably not found.

Young of the previous year — In June 1969 about 78% of the trapped animals were 1 year old. At this time the larvae entering their 2nd year were 1.5–5.5 cm in body length, with the highest proportion of them being between 4.0 and 4.5 cm long (Fig. 2). By August most of these animals were 4.5–5.0 cm long; much of the increase in mean population size during the summer was no doubt due to their growth (Fig. 2). In late August and early September a large proportion of the 2nd-year animals metamorphosed. The peak that they formed in the size distribution disappeared, and young-of-the-year formed a peak in the lower size ranges as they entered the trapped population.

Second-year animals formed almost the entire *A. gracile* population in 1 m deep areas with an open-mud bottom. In all subhabitats in the lake this age class was in the majority, although they were in relatively low proportion in deep areas and beds of *P. natans* and *Equisetum* sp.

Adults — Efford and Mathias (1969) have found that Marion Lake *A. gracile* must be at least 5.0 cm long before they possess gonads, but it appears

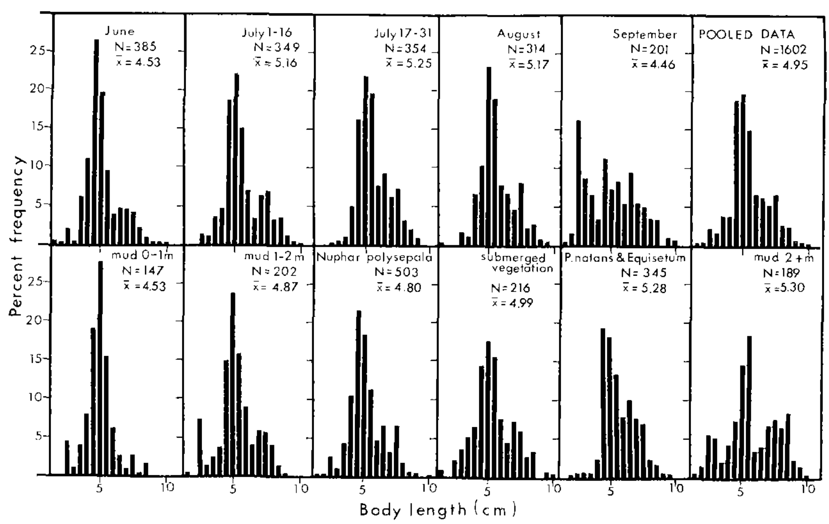

FIG. 2. *Ambystoma gracile* size frequency distributions plotted through time and between areas with different substrata.

that most animals mature at about 5.5–6.0 cm body length. This is also the size at which metamorphosis may occur. In June about 22% of the animals trapped were of adult size.

About 35% of the neotenous adult *A. gracile* caught were in open-mud areas deeper than 2 m. In these areas adults formed about 40% of the population. Few adults were caught in shallow open-mud areas.

Not all of the *A. gracile* adults breeding in Marion Lake were neotenous. In April 1969, on nine nights of observation, 106 metamorphosed and 117 neotenous adults were seen. These numbers were not significantly different from a 50:50 ratio (x^2, P = .01). Only three breeding pairs were seen, all of which consisted of a metamorphosed male and a neotenous female. It was not known what proportion of the adult population bred during the year. All metamorphosed adults appeared to have left the lake by the 1st week in May.

Taricha granulosa Population

The *T. granulosa* population was estimated at 2450 with the 95% confidence limits ranging from 2363 to 2542. The mean weight of adult *Taricha* was 7.5 g so the total lake biomass of this animal was about 18 kg. Little was discovered about the eggs and larvae of *T. granulosa*. This animal is known to lay its eggs singly or in small clumps (Chandler 1918), and females were seen laying eggs in this way in Marion Lake. The eggs were very small, however, and could not be found during diving excursions. Few *Taricha* larvae were found in the lake. These animals were too small to be caught in funnel traps frequently, and it is probable that many of those larvae trapped were erroneously identified as *A. gracile* larvae.

In early August 1969 the first *Taricha* larvae of the year were found in the lake. Four of the five larvae caught had a body length of 2.5–2.7 cm and were undergoing metamorphosis to the terrestrial stage when they were caught. One specimen caught on August 20 was 0.9 cm in length and had reached the stage of development where it had two toes on each hind foot.

The size frequency distributions of the male and female adult *Taricha* populations both approximated bell-shaped curves (Fig. 3). No seasonal changes in size class distribution could be recorded in either sex, since *Taricha* is a slow-growing animal. The mean growth rate of males is 0.93 mm/year and that of females is 0.59 mm/year (Efford and Mathias 1969). The sex ratio was not significantly different from 1:1 (t-test, P = 0.05) in the *Taricha* population as a whole and in individual centers of concentration. The size frequency distribution

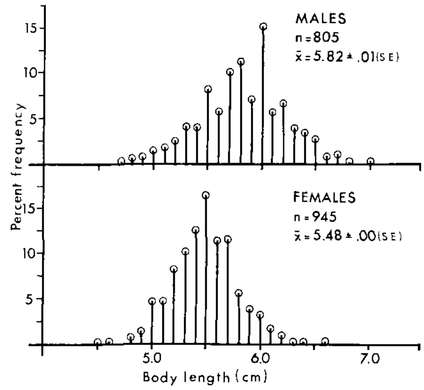

FIG. 3. *Taricha granulosa* adult size frequency distributions.

of *Taricha* appeared to be constant for the various areas as well as at different periods during the study period.

Trapability

Taricha granulosa were attracted to funnel traps. In the laboratory and in Marion Lake, newts would enter and leave traps in much the same way as they would enter and leave clumps of vegetation or fishnet. *Ambystoma gracile* did not appear to be attracted to traps and there were indications that some degree of trap-avoidance learning took place with these animals. Many trapped *Ambystoma* showed "fright" reactions such as violent swimming. This was not observed among trapped *Taricha*.

Population Distribution and Movements

Ambystoma gracile observed from a boat at night appeared to be widely dispersed. Animals seen to approach each other closely did not show agonistic behaviour, although when two animals were seen to touch, both animals would usually swim rapidly apart.

Although 504 *A. gracile* were individually marked, only 16 were recaptured. Since only five of these were caught more than 1 day after first capture, the returns were too scanty to allow any rigorous statement about how extensive individual *A. gracile* movements are. However, all recaptured animals were found in the subhabitat type that they were marked in. Furthermore, since the size compositions and trapped numbers of *Ambystoma* in individual subhabitat types did not change from early June to late August, it appeared that there were no large shifts in the *Ambystoma* population distribution except during the early spring, when metamorphosed adults entered the lake for a few weeks and during early September when metamorphosed young of the 2nd year left the lake.

The total weekly catch resulting from all methods of capture indicated that in 1969 the first *Taricha* entered Marion Lake around mid-April and the last animals left it in late September or early October (Fig. 4). There were two peaks in the catch per unit of effort–time curve, since the catch dropped off during late June and early July. During the time of peak catches amplexed pairs were common, but during the time of low catches no amplexed pairs were found.

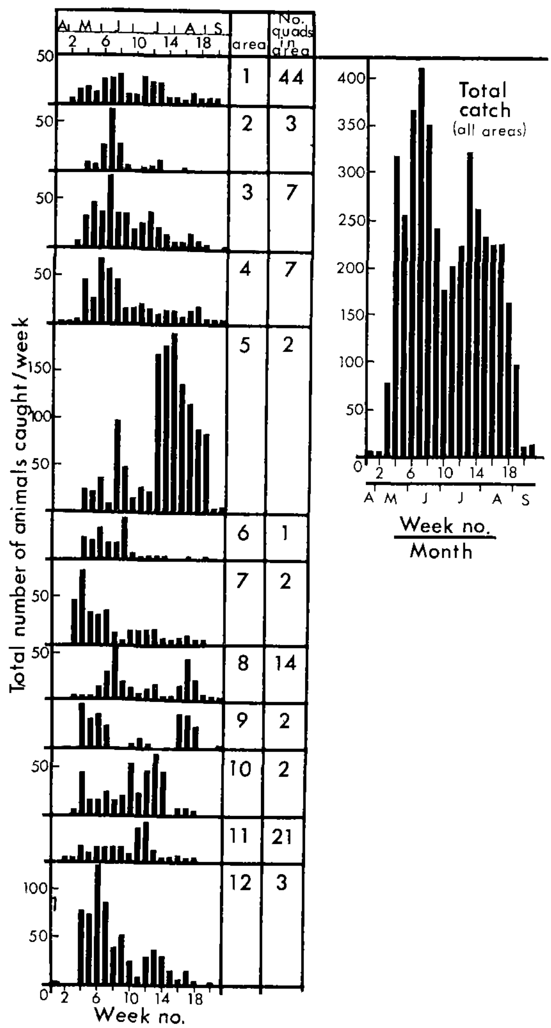

FIG. 4. Weekly catches of *Taricha granulosa* in the areas of the lake as a whole. The catches are the total result of trapping, diving, and netting from boats. During week 14 no diving was done. The probable diving catch was extrapolated from the numbers of animals caught by other methods.

The trapping data show that there is approximately a linear relation between the length of time since an animal was marked and the number of times that an animal was recaptured (Fig. 5). This suggests that many animals tended to remain in the lake throughout the season. However, the spatial distribution of the population within the lake changed through time (Fig. 4, Table 2).

The distribution of the *Taricha* catch was contagious. Large numbers of *Taricha* tended to form aggregations similar to those described by Farner and Kezer (1953) and Coates et al. (1970). In some instances up to 190 animals could be caught by hand in an area of about 15 m^2, as in area 5 during the 1st week in August. Although the location of concentration centers changed through time, they appeared to serve as a "home range" for the animals inhabiting them. Efford and Mathias (1969) found that of 315 animals they displaced, 314 returned to the site from which they were captured. A displacement experiment done by the author during July 1968 yielded similar results.

Thirty-five individuals were captured eight or more times during 1969. For each of these animals a list was made of the areas of the lake in which it was captured (Table 2). These animals all shifted their home range at least once. One animal was caught in seven of the 12 areas in the lake. The same pattern held true for animals caught fewer numbers of times. This and the stability of the population (Fig. 5) indicates that shifts in the sites of concentration centers observed during the 1969 season reflect the movements of individuals within the population and not the influx and egress of animals to and from the lake.

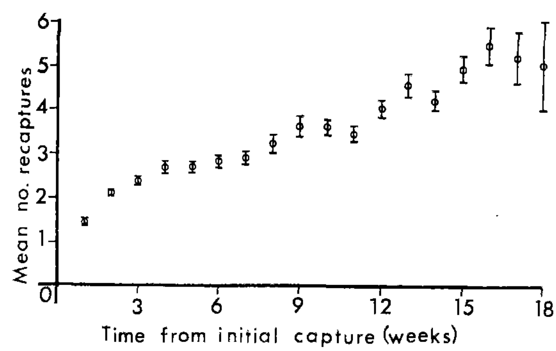

FIG. 5. A plot showing the relation between the time during which *Taricha granulosa* were marked and the mean number of times that they were recaptured. The vertical bars show standard errors.

TABLE 2. Areas of capture for *Taricha granulosa* caught eight or more times during 1969. The areas of capture are shown in chronological order.

Animal no.	Capture no. 1	2	3	4	5	6	7	8	9	10	11	Capture date (*first and last*)
1	7	7	7	5	5	5	5	5				14/5–1/9
2	7	12	7	12	5	5	5	5				21/5–19/8
3	12	12	4*a*	4*a*	12	12	5	5				21/5–26/8
4	12	12	7	12	12	1*b*	5	5				21/5–26/8
5	4*b*	6	7	6	4*b*	5	5	5				21/5–26/8
6	12	11	12	12	12	12	6	12				22/5–11/8
7	12	12	12	8	9	10	9	5				22/5–1/9
8	6	6	6	6	4*c*	6	6	10				23/5–18/7
9	1*b*	8	8	2	1*b*	3	5	5				26/5–12/8
10	12	12	12	10	10	10	10	10				28/5–18/8
11	4*b*	5	8	5	5	4*a*	5	5				2/6–1/9
12	6	5	6	4*c*	5	6	5	5				4/6–1/9
13	1*b*	2	11	12	7	5	8	3				12/6–27/8
14	12	10	9	12	5	5	11	12				14/6–21/8
15	2	3	3	3	3	3	3	3				18/6–21/7
16	7	7	7	6	5	5	5	5	5			14/5–26/8
17	7	4*b*	4*b*	5	9	6	7	5	5			14/5–26/8
18	7	4*c*	5	6	4*a*	5	5	5	5			21/5–26/8
19	4*b*	4*b*	6	4*a*	5	4*a*	5	5	5			21/5–1/9
20	12	12	12	12	5	5	10	5	5			21/5–1/9
21	3	3	3	8	5	5	5	5	5			22/5–5/9
22	9	10	9	12	11	12	11	10	9			23/5–18/7
23	12	12	12	12	11	10	10	10	10			23/5–24/7
24	12	1*b*	10	10	10	11	10	10	10			23/5–18/8
25	12	12	11	10	12	10	10	5	9			26/5–22/7
26	12	12	10	5	10	5	8	9	5			10/6–1/9
27	5	9	5	9	3	9	8	9	9	9		7/5–23/6
28	8	1*b*	12	7	12	10	10	11	10	10		14/5–6/8
29	7	5	2	3	5	9	5	5	5	5		15/5–19/5
30	9	9	12	12	12	11	12	12	5	8		20/5–15/8
31	12	12	12	7	11	12	12	3	1*b*	10		21/5–18/8
32	7	7	12	12	10	10	5	10	5	5		21/5–19/8
33	6	6	6	12	12	6	7	5	5	8		22/5–26/8
34	11	7	7	12	7	12	7	7	6	8	5	12/4–10/6
35	12	12	10	12	9	12	10	5	10	5	5	23/5–5/8

The placement of concentrations appeared to be correlated with the following factors.

Spatial complexity

All major centers of concentration were spatially complex. Areas 2, 4, 6, 7, 9, and 10 contained thick clumps of vegetation or tree roots. *Taricha* were also found in clumps of fishnet placed in the lake. The large numbers of animals caught in area 12 were almost all found clinging to a doubled layer of fishnet on a large pen built in the summer of 1967. Similarly, a piece of netting placed in area 10 during capture week 10 rapidly became a concentration center.

Temperature

In laboratory experiments *Taricha*, in water above 20 C, tended to lose their aquatic secondary sex characteristics and left the water if given the chance (Neish MS 1970). In the lake, as the surface water neared 20 C during late June, shallow water concentration centers disappeared and large numbers of animals were found in deeper areas where the temperature was about 15 C.

Social interaction

The presence of *Taricha* at a concentration center may have attracted other *Taricha*. During capture week 15, 30 newts were placed in a cylindrical cage of hardware cloth. A clump of $\frac{3}{4}$-inch fishnet was draped around this cage. Although no animals established themselves on the netting, a number of animals established themselves in a *P. natans* bed immediately adjacent to it, and when the cage was removed this concentration center ceased to exist. Twitty (1966) has shown that *Taricha torosa* males are attracted to females through the use of pheromones. In Marion Lake *T. granulosa* males were attracted to other males as well, at least to the point where homosexual amplexed pairs were occasionally seen. Few amplectic pairs were seen in clumps of *Taricha* in concentration centers, so these aggregations may not have been simply breeding aggregations.

Prey

During the 4th week of trapping, large numbers of *R. aurora* tadpoles hatched in areas 9 and 10. At this time *Taricha* appeared in these areas and were found to be eating tadpoles. As the tadpoles dispersed there was a decrease in the number of *Taricha* caught.

Mortality

Taricha granulosa was not eaten by the fish in Marion Lake, but *A. gracile* were found in the stomachs of rainbow trout (Efford and Mathias 1969), and one specimen was seen in the process of being eaten by a diving bug (*Lethocerus americanus* (Leidy)). The potent poison possessed by *Taricha* (Brodie 1968) makes it unlikely that newts were eaten by the mink, heron, or mergansers that periodically frequented the lake, although some *Ambystoma* may have been eaten by these animals. *Ambystoma gracile* in the process of regenerating limbs and tails were frequently captured in the lake, but this was never the case with *T. granulosa*. No dead *Taricha* were found in the lake although dead *Ambystoma* were occasionally found. These specimens were rapidly consumed by carrion feeders (such as tadpoles and amphipods) or were decomposed.

Discussion

The *T. granulosa* adult population size estimate made during the present study was similar to Efford and Mathias' (1969) estimate of 3965 individuals. In the present study a large proportion (about 83%) of the population was marked, so the estimate of 2450 individuals can probably be regarded with some confidence.

The *A. gracile* population estimate of Efford and Mathias (2300 individuals) differed radically from the present estimate of 14,500 adults and 45,000 2nd-year larvae. Efford and Mathias' estimate was based on the ratio of *T. granulosa* to *A. gracile* captured in funnel traps. Acceptance of such a method depended on the assumption that the two species were equally trappable. This assumption was not tenable, since *Taricha* appeared to be attracted to traps and *Ambystoma* to have avoided them to some extent. Avoidance learning has been demonstrated in *Ambystoma punctatum* (Schneider 1968), and the failure of Efford and Mathias to obtain consistent trapping records in areas repeatedly trapped to saturation may have been due to this phenomenon, as they suggested.

According to the present estimate there were about 6000 *A. gracile*/ha in Marion Lake, excluding young-of-the-year. This is high when compared to the densities of 41–3238/ha recorded among terrestrial adult salamanders (Anderson 1960; Hendrickson 1954; Stebbins 1954), but it must be remembered that the present census included 2nd-year larvae. There were about 1450 neotenous adult *A. gracile*/ha in the lake.

The large estimate of *A. gracile* numbers was not expected on the basis of trapping results and daytime observations. The nocturnal feeding habits of these animals and the short time during which they are exposed as they hunt (Neish MS 1970) make *Ambystoma* inconspicuous except during the early hours of darkness, when most salamander feeding occurred. Personal communications from researchers working in lakes in British Columbia and northern Manitoba suggest that neotenous *A. gracile* and *Ambystoma tigrinum* may be abundant in many lakes. Efford (1970) has estimated that *A. gracile* accounts for about 55% of the benthic predation by salamanders and fish in Marion Lake. This means that in Marion Lake *Ambystoma* is a significant predator.

Although *T. granulosa* is not nearly so abundant as *A. gracile* in Marion Lake, it may still have a significant effect as a predator since there was evidence that *Taricha* tends to concentrate its predation in small areas. The incursion of newts into tadpole hatching areas is an example of the response of *Taricha* to prey in high density. Such invasions may have a great effect on prey mortality (Neish MS 1970; G. Calef, personal communication); and predation behavior of *A. gracile* and *T. granulosa* is considered in detail in Neish (MS 1970).

It was estimated that in Marion Lake there were about 14,500 *A. gracile* of a size consistent with the possession of gonads, yet only about 750 egg masses were counted. The reasons for the discrepancy between the number of egg masses and the estimated number of adults could not be explained since little is known about breeding behavior of mixed neotenous–metamorphosed *A. gracile* populations. Calef (personal communication), in working on the breeding chorus of *R. aurora* in Marion Lake, has also found a low number of egg masses/adult population ratio. Anderson (1960) found a similar disparity in populations of the salamanders *Batrachoseps attenuatus* and *Aneides lugubris*, associated with high population density and resorption of eggs by females.

The distributions of *T. granulosa* and *A. gracile* were different, with the latter having a widely dispersed, apparently stable distribution, whereas the former had a highly contagious distribution that underwent drastic changes throughout the spring and summer. Dispersal of the *A. gracile* population may have been related to *Ambystoma*'s tendency to snap at each others' limbs and gills, which resulted in the two animals involved swimming away from each other. In the laboratory the loss of limbs and gills was fairly common. This was not the case with *T. granulosa*. Neither in the laboratory nor in the lake did *A. gracile* gather in closely knit masses similar to those commonly found among *T. granulosa*.

Coates et al. (1970) described a large concentration of *T. granulosa* in Clear Lake, Oregon, and concluded that the aggregation was postreproductive. Concentrations of animals in Marion Lake were seen during the entire study period, and amplectic pairs and egg-laying females were found both in and near centers of concentration, so they cannot be regarded simply as a postreproductive phenomenon.

An outstanding characteristic of the distribution of *T. granulosa* is that considerable changes were observed as the year progressed, both in the numbers of animals in the lake and in the location of concentration centers; no *Taricha* could be found before mid-April and after late September, and the catch per unit of effort decreased during late June and early July. At this time animals may have been wandering in and out of the lake (Pimentel 1961). Coincident with the decrease in the *Taricha* catch was an absence of amplectic pairs and a decrease in the volume of fish stomach contents observed by Sandercock (MS 1969) and a drop in macrophyte productivity observed by Davies (1970).

All concentration centers were found in complex areas such as tangled vegetation or fishnet. Changes in the locations of concentration centers appeared to be related to the effects of temperature and prey abundance. Shallow water concentrations disappeared as temperature rose during the late spring, and new concentrations formed in cooler, deeper areas. Depth alone probably did not restrict the distribution of *T. granulosa;* large concentrations have been found at depths up to 40 ft in Loon Lake, B.C.

Movements of individual *Taricha* suggest an appraisal of the term "home range" in connection with these animals. Displacement experiments of Efford and Mathias, as well as those done in the present study, indicate that *T. granulosa* rapidly returned to the point from which they were removed. It was evident that *T. granulosa* homed through water, unlike *T. torosa*, which homed over land (Twitty 1966). The home ranges to which the animals returned can at best be described as temporary, however, since some animals were caught in seven areas of the lake in 21 weeks, and most of the animals caught five or more times were captured in more than one area.

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