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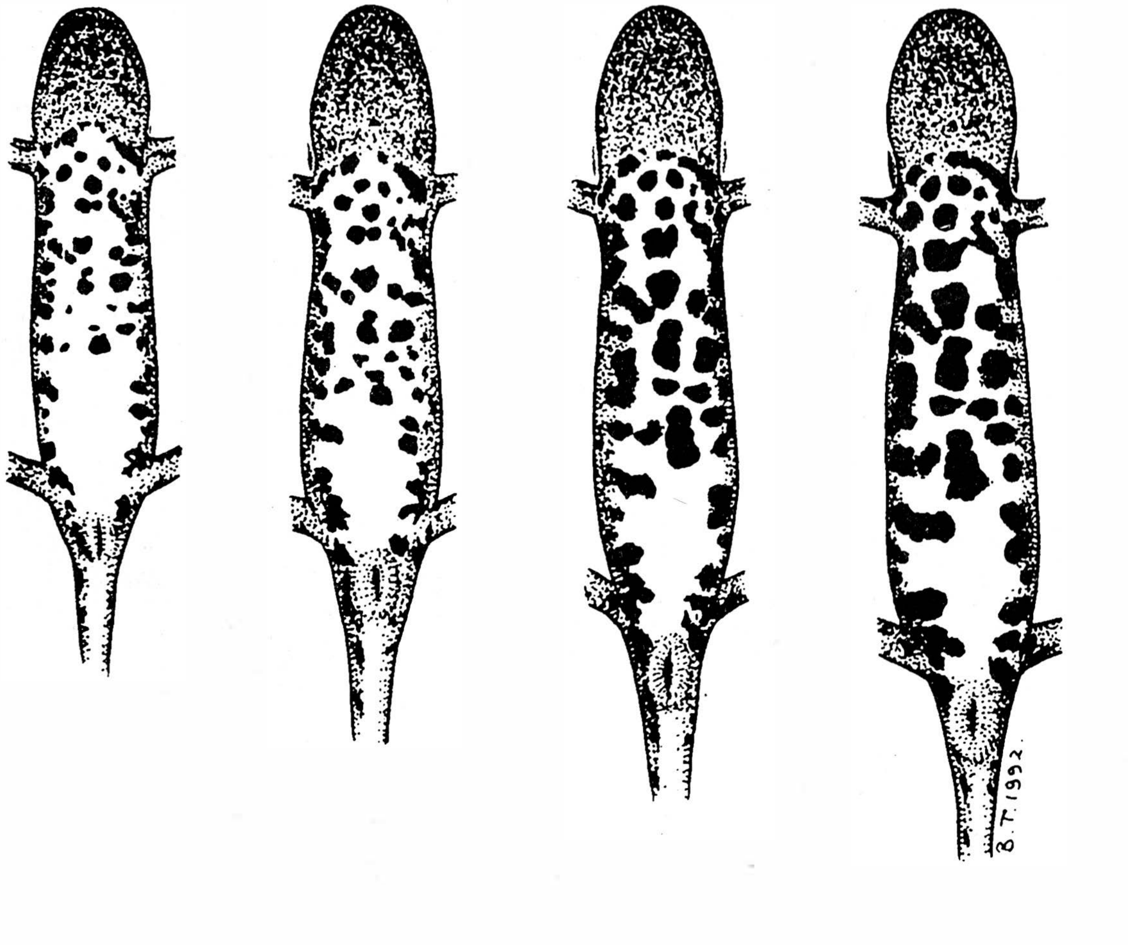

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A SIX YEAR STUDY ON THE POPULATION DYNAMICS OF THE CRESTED NEWT (*TRITURUS CRISTATUS*) FOLLOWING THE COLONIZATION OF A NEWLY CREATED POND

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ABSTRACT

The population dynamics of the crested newt, *Triturus cristatus*, in a newly created aquatic habitat in a dune area in northwestern France was studied over a six year period. After a rapid colonization of the pond in year 1, and a fast initial increase to reach 335 newts in year 5, the adult population size dropped dramatically to 16 in year 7. Variation in the adult population among years was largely due to variation in juvenile recruitment. In the longer term, the population stabilized at about 40 newts. Since the population has survived for five times the minimum generation time of the species, the colonization was judged to be a success. An estimated 50% of the juveniles joined the breeding population at age 2; those that did not breed by then spent the third year on land. The average annual survival rate for the juveniles was 0.22. For the adults survival was 0.49 and showed almost no fluctuations over time or with age. Given a short distance to disperse, the crested newt can be an opportunistic species.

INTRODUCTION

In the historic past amphibians have been favoured by agricultural practices. More breeding sites became available through the creation of ponds for cattle drinking. Also the terrestrial component of the amphibian habitat was favourable because of diversification in land use. This trend is now in reverse, mainly as a result of the intensification of agricultural practice. Field size enlargements, urban extensions and an increase in monoculture have reduced the diversity and availability of terrestrial habitat. In areas under continuous agricultural use there has been an increase in the arable to pasture ratio, with a concomitant decline in numbers of amphibian breeding sites (Oldham & Nicholson, 1986). Additionally, widespread improvement of pasture has increased soil nutrient levels, accelerating the rate of eutrophication, hydroseral succession and consequent loss of water bodies from grassland (Beresford & Wade, 1982). The loss of ponds and the decrease in terrestrial habitat suitable for amphibians are synergistic effects, and movements between local populations becomes increasingly difficult. Extinction probabilities may increase significantly with increased interpopulation distance (Sjögren, 1991; Sinsch, 1992).

In the United Kingdom a national survey of one species, the crested newt, *Triturus cristatus*, has shown a decline in breeding sites of 37% during ten years, attributable mainly to agricultural development and pond neglect (Oldham & Nicholson, 1986). Extensive studies in northwestern Germany have shown *T. cristatus* to be the rarest of the four indigenous newt species (Blab & Blab, 1981; Feldmann, 1981). It was found almost exclusively in ponds where other newt species also occurred. Similar observations were made in Denmark, Switzerland and northwestern France (Arntzen & Gerats, 1976; Grossenbacher, 1977; Bisgaard *et al*., 1980). Clearly, *T. cristatus* has habitat requirements that are more demanding than that of most other palaearctic newt species. One consequence of a specialized habitat choice might be that for dispersal fewer 'stepping-stones' are available for such a species than for those with less stringent ecological requirements. This raises the question of how successful the crested newt can be in colonizing new habitats for breeding. This is particularly important in view of programmes at the more practical side of nature conservation that aim to improve aquatic and terrestrial habitats and create new ponds. In the present paper we describe the colonization of a new pond by *T. cristatus* and we followed the success of the newly established population.

MATERIAL AND METHODS

SITE DESCRIPTION

The study was carried out in an abandoned sand-quarry in a coastal dune system in northwestern France (Fig. 1). The quarry is located in the département (province) Pas-de-Calais, approximately 1 km southeast of the village of Ambleteuse and 800 m from the sea. The quarry pond was discovered as an amphibian breeding site in 1975, at which time it was shallow relative to its area and almost devoid of macrophytes (maximum surface approximately 160 m^2, maximum depth 30 cm). For two years the only amphibian species observed to be

Fig. 1. Study pond in abandoned quarry in northwestern France. The part of the pond in the foreground is an original dune slack; that in the background is newly created (Photo: H. Kersten).

year	number of visits	first visit	last visit	total catch	different individuals caught	$\hat{N}$±SE[a]	sampling efficiency[b]	observer[c]
1979	3	24 April	18 June	40 adults	40	c. 60	c. 2 out of 3	WW & AZ
1980	8	8 April	3 Sept.	70 adults	70	c. 105	c. 2 out of 3	FH & AZ
				23 juveniles (age class 0+)[d]	23	-	-	
				178 juveniles (age class 1+)	150	309±49	49%	
1981	7	14 March	14 May	283 adults	153	169±15	91%	ST & JA
1982[e]	6	5 April	5 July	335 adults	235	346±35	68%	HK & JA
				35 juveniles	26	44±17	59%	
1983[e]	11	20 March	18 May	706 adults	201	182±9	100%	HK & JA
				19 juveniles	15	23±16	65%	
1984	3	27 April	29 April	22 adults	14	16±6	88%	JA & HK
				0 juveniles	0	0	-	
1992	8	8 April	1 June	94 adults	53	55±10	96%	CA & JA
				0 juveniles	0	0	-	

TABLE 1. Recording programme and estimates of sampling efficiency and population size of *Triturus cristatus* in a pond in northwestern France. *Notes*: a, determined by capture-recapture approach (weighted mean method of Begon (1979)). For 1979 and 1980 estimates see text. b, No. individuals caught/estimated population size x 100. For 1983 maximum estimate of population size ($\hat{N}$±2 SE) is used instead of $\hat{N}$. For 1979 and 1980 estimates see text. c, initials; to identify observers see acknowledgments and authors names. d, specimens just metamorphosed, captured on September 3 (see text and Fig. 2). e, see Kersten (1984) for a more detailed account.

breeding in it was the natterjack toad (*Bufo calamita*). At this time, the absence of crested newt eggs from the pond suggested that a breeding population had yet to be established. Eggs deposited by crested newts are easy to spot and can be distinguished from eggs of the other newts species occurring in this part of France (Arntzen, 1990). In the summer of 1977 the pond was enlarged. An excavation (7 x 20 m, maximum depth > 1.2 m) was made at the eastern side of the original pond, approximately doubling its surface (Fig. 1). Three ponds inhabited by crested newts, as observed in 1975 and in later years, are situated at distances of between 120 to 360 m to the south and southeast of the quarry.

METHODOLOGY

The presence of *T. cristatus* in the study pond was noted for the first time in 1978. The population of crested newts was studied over six consecutive years (1979-1984) and in 1992. In the spring of 1979 and 1980 adult newts were counted, while from summer 1980 to 1984 the population was studied in more detail through a capture-recapture approach. In 1981, 1982, 1983 and 1992 the crested newt population was followed over a major part of the aquatic season, including the period when most adult newts were expected to be in the water (at this latitude the second half of April and the first half of May (Kowalewski, 1974; Blab & Blab, 1981; Verrell & Halliday, 1985)). In 1984 the capture-recapture experiment was confined to the end of April. Metamorphosing specimens, hereafter called 'efts' (characterized by the presence of remnants of gills) appeared in late summer and are about six months old (age class 0+). Efts were recorded in 1980 only, when the study was continued into September. The size of the aquatic portion of the juvenile cohort, efts excluded, was estimated each year, from 1980-1984. Details of the recording programme are given in Table 1.

Crested newts were detected by torching the shallow part of the pond in the period from dusk to midnight and caught by hand or by using a dip-net. All newts were classified as adults (with distinct male or female secondary sexual characteristics), juveniles (with no or indistinct such features) or efts. Snout-vent length (SVL) was measured on plastic coated millimetre graph paper, from the tip of the snout up to and including the insertion of the hind legs. For practical purposes this measurement of body size is the same as the more widely used measurement up to and including the anterior edge of the cloacal opening. To allow individual recognition upon recapture, the belly pattern of the newts (an irregular array of black spots on a yellow or orange background) was recorded photographically (Hagström, 1973). Efts and juveniles had generally not yet fully developed the highly individual distinctive patterns as found in the adults, and consequently individual recognition was more difficult. In almost all the juveniles, however, sufficient clues were available either from spots on the belly, mostly on the anterior side of the body between the fore-legs, or, if these were absent, from the pattern marking the ventrolateral margin of the belly. Photographs were taken in the field and the newts were released immediately.

A null hypothesis of random catch was tested for males versus females by comparing the number of each sex among specimens captured for the first time with the number of recap-

year	captures		recaptures		sex-biased catchability[a]	sex-ratio[b]
	males	females	males	females		
1979	18	22	-	-	-	0.82
1980	32	38	-	-	-	0.84
1981	79	74	71	59	NS	1.13
1982	115	120	49	51	NS	0.96
1983	100	101	249	256	NS	0.98
1984	7	7	8	0	**	2.14
1992	25	28	18	23	NS	0.84
total	376	390	395	389	NS	0.99

TABLE 2. Number of captures and recaptures for male and female *T. cristatus*. No significant differences (P>0.05) were observed in the catchability of males and females in the years that population size estimates were made (except for 1984). Sex ratio is not significantly different from unity in all cases. *Notes:* a, one-tailed G-test of independence; NS, P>0.05; **, P<0.01. Williams' correction for continuity is applied in case sample size is small. b, sex ratio is expressed as total no. males / total no. females and tested against unity by G-test goodness-of-fit.

tured specimens (Arntzen & Hedlund, 1990). Total population size ($\hat{N}$) was estimated for each year in which capturing - recapturing experiments were done, using the weighted mean algorithm of Begon (1979) for adults and juveniles separately. Sampling efficiency was calculated for both groups in each of these years by dividing the estimated population size by the total number of different individuals caught that year. These figures were used to obtain an estimate of the number of recaptures from previous years had sampling efficiency been 100 %. This value in turn was used to estimate yearly survival rate (S).

To determine the age of the newts two methods were used: (i) directly, by capture and later recapture of one year old juveniles (age class 1+, see below for initial age determination), and (ii) indirectly, on the basis of observed population structure. Because the population was a newly established one, we infer that no newts hatched in this pond prior to 1977 and conclude that adults observed in 1979 (with the exception of occasional immigrants) had age ≤ 2, adults caught in 1980 had age ≤ 3 etc. Since adult crested newts were at least two years old (two years being the minimum age of maturation observed in the wild (Dolmen, 1983*a*; Francillon-Vieillot *et al.*, 1990; and present study)), it can be concluded that adults in 1979 *were* two years old, while adults in 1980 were 2.5 ± 0.5 years old, adults in 1981 were 3 ± 1 years old, etc., with the accuracy of the estimate declining with more year classes contributing to the population. So, by combining a high sampling efficiency, a high recapture rate and some knowledge of the onset of the population expansion, we circumvented the tedious techniques that are generally used for aging newts (Francillon-Vieillot *et al.*, 1990).

RESULTS

JUSTIFICATION OF METHODS

The number of crested newts observed is given in Table 2, partitioned for specimens captured for the first time (with or without being recaptured later on in the same year) and recaptures. In three cases out of four no significant departure from the expected pattern of random catch was observed. In all years the observed sex-ratio was close to unity, bolstering our confidence that the method used to detect and catch adult newts is essentially unbiased. A deviating pattern with no females recaptured was observed in 1984. In accordance with the effort put into it, the sampling efficiency for juveniles was inferior to that for the adults (Table 1).

A histogram of the body-size for all newts captured in 1980 is presented as an example (Fig. 2). The histogram shows a distinctly bimodal distribution, in which the large animals are adults and the smaller animals are efts and juveniles. Within the latter group a bimodal size distribution is observed when samples for the third week of July are compared with the sample from the first week of September (Fig. 2 insert). The latter group consists almost exclusively of efts. The larger sized juveniles, clearly forming a single cohort, hatched in the preceding year and hence were about 18 months old (age class 1+, see below).

The belly pattern of *T. cristatus* can be shown not to be fixed. Both the number of black dots and their size tend to increase over time. However, change is gradual and we are confident in having correctly identified all adult specimens and all those juveniles that were recaptured within the season, or in the next year; recognition of a young animal in a subsequent year, however, may be problematical. For instance, to establish the identity of the 1980 juvenile depicted in Fig. 3 in 1982 and 1983 (Fig. 3 *c,d*) would have been difficult if the 1981 record had not been available. The high sampling efficiency in a population of moderate size helped to narrow down the number of unrecorded animals which in turn increased the reliability with which the juveniles could be identified. Summarizing the above points, we claim correct recognition of adults as well as juveniles (excluding efts) within a season and beyond, provided that no gaps exist in the annual recording.

JUVENILE GROWTH, MATURATION AND BREEDING

As shown in Fig. 2 growth of juveniles over the summer was fast with an average increase of SVL of 8.3 mm in 10 weeks. Assuming growth continued at this rate until early September and slowed down towards hibernation, a body size increase with another 6 mm to almost adult SVL of 52 mm by

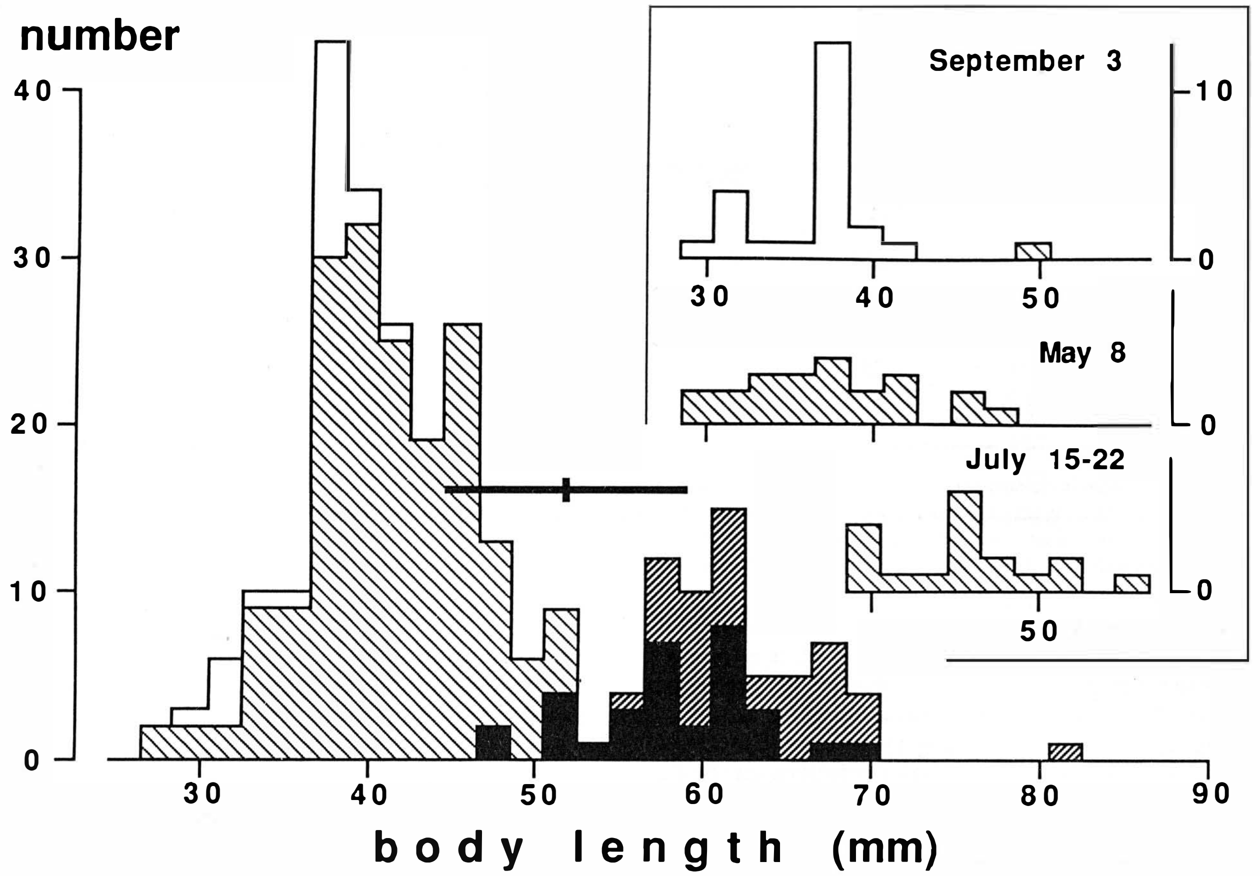

FIG. 2. Histogram of body-size for *Triturus cristatus* collected in 1980. Histograms are additive. Adult specimens are indicated by black bars (*males*) and densely shaded bars (*females*); newly metamorphosed juveniles (*efts*) are indicated by white bars and juveniles of age class 1+ by lightly shaded bars. The insert shows the size distribution of (almost exclusively) efts in September and juveniles of age class 1+ in May and July. The horizontal bar shows mean and range of the hypothesized size distribution of juveniles towards hibernation at the end of their second year, demonstrating that approximately half of the cohort may by then have reached adult size (details see text).

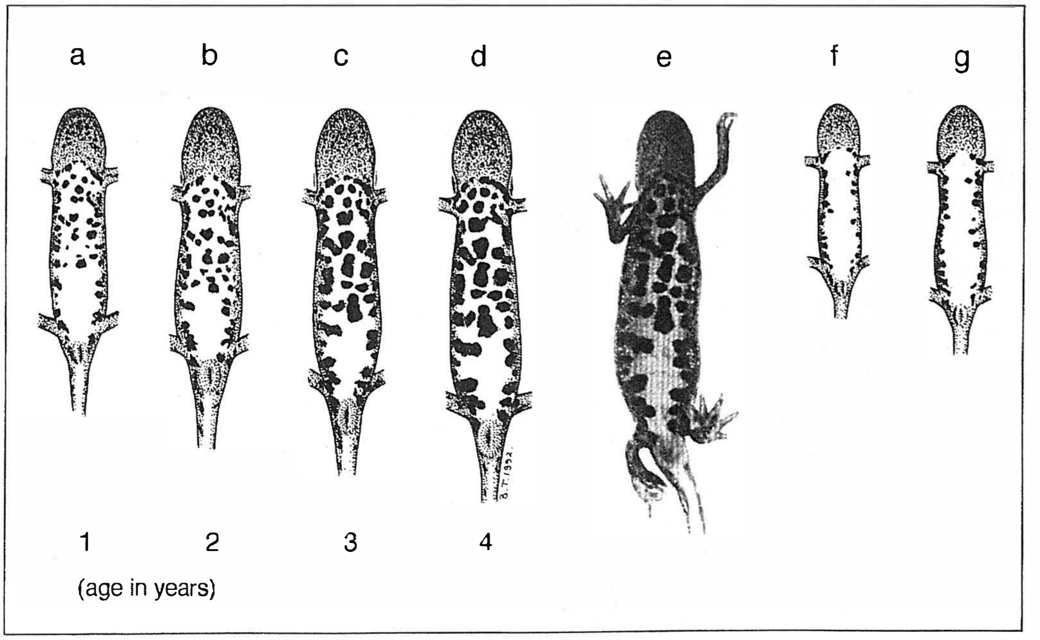

FIG. 3. Development of the belly pattern of a female *Triturus cristatus* over four consecutive years. Note that it would have been difficult to recognize the adult specimen in years 4 and 5 (C and D) from the juvenile belly pattern in year 2 (A) had not the specimen been recorded in the intervening year (B). The drawings are taken from photographs (compare D and E). Particularly indistinctive juveniles (G and H) can be identified by their ventro-lateral patterning, even in the absence of mid-ventral spots.

the start of the third year would be expected (Fig. 2). Of the 30 juveniles that were observed over three 2-year periods (1981-1982, 1982-1983, 1983-1984) all had matured by the year of recapture (17 were males and 13 were females). Average SVL (± SD) of these young adults was 58.5 ± 5.6 mm and 61.4 ± 4.4 mm for the males and females, respectively. These data indicate that all specimens that come to the pond in their third year have become sexually mature. Interestingly, these recruits to the breeding population were on average significantly larger as juveniles than their cohort counterparts that were not observed to join the breeding population (SVL 44.4 ± 4.0 mm (n=30) compared to 42.0 ± 5.3 mm (n=202); P<0.05 in t-test), suggesting that rapid growth and early maturation are in some way related.

Of the ten animals in 1982 that had been previously caught in 1980, eight were also observed in the intervening year 1981. Considering the efficiency of sampling in 1981 (91%), this is about the number expected under the null hypothesis that all adult crested newts come to the pond to breed each year. A similar observation can be made regarding the data of 1981 to 1983, when ten specimens out of 51 where not observed in the intervening year 1982 when sampling efficiency was 68%. These data taken over two 3 yr periods support the notion that the entire adult population of crested newts is present in the pond every year (Table 3). No significant difference was observed for male and female newts (G-test of independence, P>0.05).

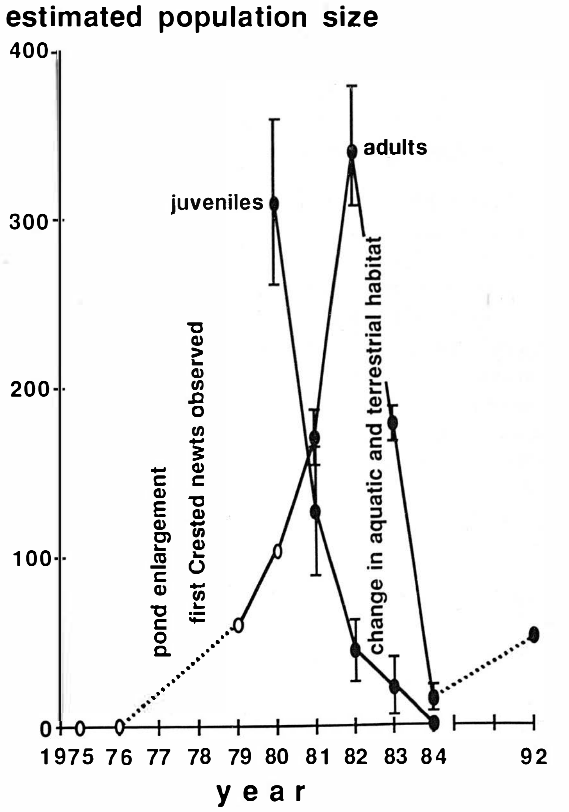

FIG. 4. Development of population size of *Triturus cristatus* over the period 1975 to 1982. Solid dots refer to population size estimates made by capture - recapture experiments. Bars indicate the standard error of the estimate. Open dots refer to less rigorous estimates (details see text).

year	capture	recapture two years later	intervening year specimens observed[a]	intervening year specimens not observed
1980	juv./male	male	3	0
	juv./female	female	5	2
	total		8	2
1981	juv./male	male	16	5
	juv./female	female	25	5
	total		41	10

TABLE 3. Capture-recapture data for *Triturus cristatus* over two 3-yr periods. In both cases the number of specimens not observed in the second year is not significantly different from expected (P>0.05[b]). Expectations are drawn from sampling efficiency (see Table 1), testing the null hypothesis that adults breed every year. *Notes*: a, note that all juveniles observed in the second, intervening year were classified as adults in the third year; b, one-tailed G-test of goodness of fit is applied with Williams' correction for continuity if the sample size is small.

POPULATION DEVELOPMENT

The first population size estimate for adults on the basis of capture-recapture data was made in 1981 ($\hat{N}$ = 169, Table 1). In 1982 the population size had gone up to approximately 350 individuals ($\hat{N}$ = 346, SE = 35). In 1983 the population was down to about 180 individuals. A dramatic drop in population size was observed in 1984, when $\hat{N}$ was down to 16 adults. In 1992 the population was estimated at 55 adults. In each of the years sampling efficiency was high, ranging from an estimated 68% in 1982 to approaching the 100% level in 1983 (Table 1).

In the absence of recapture data, only a rough adult population size estimate could be made for 1979 and 1980. To this end we assumed a catching rate lower than that obtained for adults in the years 1981-1984 (when sampling efficiency averaged 85%, weighted value) since less effort was made these years. On the other hand sampling efficiency must have been substantially higher than that for the juveniles (1980 - 1983 : 49%, weighted value). At the intermediate catching rate of two out of three, the population size for 1979 can be estimated at roughly 60 individuals. Applying the same catching rate to the figure of 1980, a population size estimate of $\hat{N}$ = 105 is obtained. The juvenile cohort in 1980 was estimated from capture-recapture data to equal approximately 300 individuals. In the years following, the number of juveniles in the pond went down gradually to reach a zero level of observation in the year 1984. Data on the development of the newt population over a 18-year period are summarized in Fig. 4.

SURVIVAL

Altogether 540 individuals (273 males and 267 females) were captured that were not recorded in any of the subsequent years; 71 males and 88 females were recaptured between years.

With the exception of 1984, when only a single newt was recaptured out of the 216 different specimens recorded in

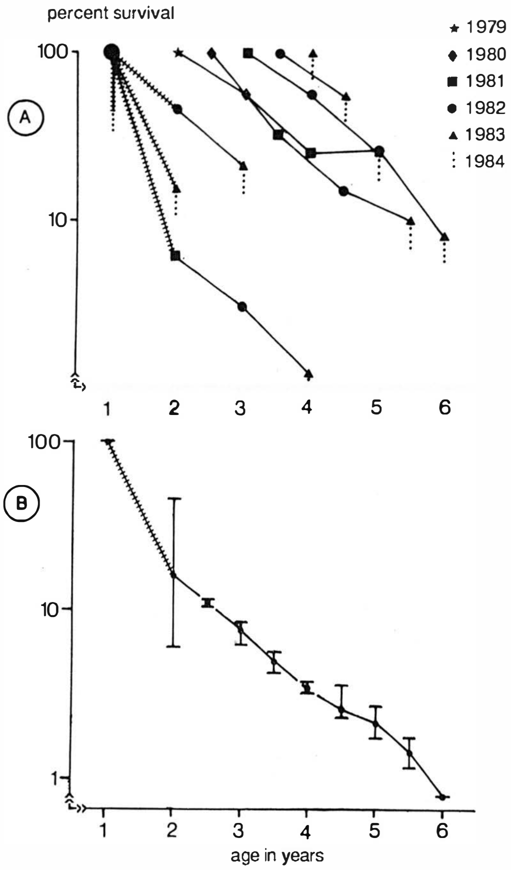

FIG. 5. Survivorship curves of *Triturus cristatus*. Juvenile survival is indicated by barred lines, adult survival by solid lines. The survival rate of juveniles is likely to be an underestimate (details see text). (A) Year to year comparisons for eight cohorts; (B) totals over the years, per half year, excluding the data for 1983 to 1984 when survival rate was close to zero. The observed range is indicated by vertical bars. Note that the *y*-axis has a logarithmic scale.

1983, the survival rate of adult newts (S_a) from the year of initial recording to the following year ranged from 33% for 1980-1981 to 57% for 1979-1980 (Table 4), averaging at 48% (weighted mean = 47%). Taking the recaptures over the subsequent years also into account, but again excluding the aberrant results for 1983 - 1984, S_a was 51% (weighted mean = 47%). No significant difference was observed in the yearly survival of males and females (Table 5). Survivorship curves are presented in Fig. 5. From the approximately parallel running lines in Fig. 5*a*, and from the straight line that can be drawn through the data points in Fig. 5*b* it can be concluded that S_a shows little variation with adult age. For the whole of the study S_a was estimated at 49%. For juveniles S ranged from 7% for 1980 - 1981 to 45% for 1981-1982 (Table 4) averaging at 22% (weighted mean = 17%).

DISCUSSION

Neither eggs nor adults of the crested newt were observed in the pond in 1975 and 1976. Breeding was observed in the spring of 1978, but may have occurred in 1977, the year that the pond was enlarged. By comparing the size of the adults as measured in 1977 against the growth curve for this population (J. W. Arntzen, in prep.) four animals (three males and one female) stand out. Their large size makes it unlikely that they hatched in the quarry pond (considering its age) and we assume that these newts are colonizers from nearby ponds. Considering the small population sizes in neighbouring ponds it is unlikely that they would have supplied more than a few adult newts. We therefore argue that a breeding population became established in 1977. This makes the crested newt a rapid colonizer in this sandy habitat. Evidently some of the colonizers were adults. No data are available for juveniles that seem to be mainly responsible for dispersal in other amphibian species (Gill, 1978*a,b*; Berven & Grudzien, 1990). A similar rapid colonization of newly created ponds in an agricultural environment was reported by Lenders (1992). Within a year of construction all four newt species locally present (*T. alpestris, T. cristatus, T. helveticus* and *T. vulgaris*) had colonized a set of six ponds at distances of up to 300 m from an existing pond. All these species were present in all the dune ponds neighbouring the quarry, although *T. helveticus* was locally rare (Arntzen, 1986). *T. alpestris* was observed for the first time in the quarry in 1981. Joly & Miaud (1989) reported a remarkable breeding site fidelity for *T. alpestris*, that might explain its late arrival, but unfortunately no comparisons were made with other newt species. Crested newts may be found at distances of up to 800 m away from their breeding ponds (Simms, 1969; Viertel, 1976). Studying the colonization rate of a large number of newly created ponds it was found that all ponds colonized by the crested newt were situated within 1000 m from a locality known for the species (Laan & Verboom, 1990). Dispersal rate was estimated at an average of 1 km per year (Arntzen & Wallis, 1991). The fact that a large population increase can occur as in the quarry pond suggests that *T. cristatus* can be an opportunistic breeder and may forage and reproduce in new ponds given the opportunity and it suggests that the difficulties *T. cristatus* may have establishing itself in new habitats (see for example Hagström, 1980*a*) originate from its localized distribution rather than from poor colonizing abilities *per se*.

As illustrated by the data from 1980 (Fig. 2), four groups of aquatic crested newts could be recognized: adult males, adult females and two cohorts of immatures ('juveniles' and 'efts'). These were the same groups as Dolmen (1983*a*) identified in an extensive study on the population structure of this species in Norway. Hagström (1977, 1979), also working in Scandinavia, concentrated on the adult stages, as the belly patterns of most juveniles could not be used for unequivocal individual recognition. Compared to Swedish crested newts, juveniles from the study site appeared to have a more obvious ventral spotting, all showing a unique ventral pattern, although with varying degrees of distinctiveness (Fig. 3; cf. Hagström 1977 : Fig. 6).

With the possible exception of 1980, less attention was given to the sampling of juveniles compared to adults, explaining the relatively low calculated sampling efficiency for the former (Table 1). Three additional factors affecting sampling efficiency that apply more strongly to juveniles than to adults could be: (i) size - the small size of juveniles could make them more difficult to detect; (ii) behaviour - the juveniles may behave differently from the adults, for example they may avoid the shallow part of the pond where adults forage; (iii) aquatic mode - where it is known that adults are aquatic over most of the breeding season and beyond and hence do approximate a 'closed population', juveniles - mostly leading a terrestrial life (Hedlund, 1990) - may stay in the pond for a short while only, where recorded animals may

year of initial capture	no. of different specimens caught	year of recapture	age at year of recapture	estimated age in year of recapture[a]	no. of recaptures[b]	survival relative to previous year: observed	survival relative to previous year: expected	estimated yearly survival rate
1979	40	1980	≤3	3	15 (22)	38%	57%	57%
		1981	≤4	4	9 (10)	23%	25%	45%
		1982	≤5	5	7 (10)	18%	26%	100%
		1983	≤6	6	3	8%	8%	30%
		1984	≤7	7	0	0%	0%	0%
1980	23[c]	no recapture data due to our inability to individually recognize efts from their belly patterns						
	150[d]	1981	2	2	9 (10)	6%	7%	7%
		1982	3	3	4 (6)	2%	3%	60%
		1983	4	4	2	1%	1%	33%
		1984	5	5	0	0%	0%	0%
	70	1981	≤4	3.5±0.5	21 (23)	30%	33%	33%
		1982	≤5	4.5±0.5	7 (10)	10%	15%	43%
		1983	≤6	5.5±0.5	7	10%	10%	70%
		1984	≤7	6.5±0.5	0	0%	0%	0%
1981	56[d]	1982	2	2	17 (25)	30%	45%	45%
		1983	3	3	12	21%	21%	48%
		1984	4	4	0	0%	0%	0%
	153	1982	≤5	4±1	58 (85)	38%	56%	56%
		1983	≤6	5±1	38	25%	25%	45%
		1984	≤7	6±1	0	0%	0%	0%
1982	26[d]	1983	2	2	4	15%	15%	15%
		1984	3	3	0	0%	0%	0%
	235	1983	≤6	4.5±1.5	104	44%	44%	44%
		1984	≤7	5.5±1.5	1	0%	0%	0%
1983	15[d]	1984	2	2	0	0%	0%	0%
	201	1984	≤7	5±2	1	0%	0%	0%

TABLE 4. Survivorship of *Triturus cristatus* over a six year period. *Notes*: a, on the (substantiated) assumption that juveniles have age 1 and adults have age ≥2 in the year of initial capture (for details see text); b, number of recaptures expected when no animals escape detection are in parentheses; c, newly-metamorphosed newts (efts); d juveniles (efts excluded).

year of first capture	recaptured in subsequent year(s): males	recaptured in subsequent year(s): females	not recaptured in subsequent year(s): males	not recaptured in subsequent year(s): females
1979	5	10	13	12
1980	8	14	24	24
1981	28	23	51	51
1982	30	40	85	80
1983	0	1	100	100
total	71	88	273	267

TABLE 5. Capture-recapture data for *Triturus cristatus*. No significant differences (P>0.05) were found in capture-recapture rate applying a one-tailed G-test of independence (1983 sample too small for testing).

Country, area	S	method	reference
Sweden, Gothenburg	0.78	A	Hagström (1979)
United Kingdom (?)	0.42	?	Frazer (1983)
Germany, Westphalia	0.50	A	Glandt (1981)
France, Mayenne	0.65	B	Francillon-Vieillot *et al.* (1990)
Sweden, Öland	0.65	A	Hedlund (1990)

TABLE 6. Published rates of yearly survival (S) for adult *Triturus cristatus* as estimated from A, capture-recapture studies; B, age distribution (see survival curve in Arntzen & Hedlund, 1990: Fig. 3).

Country, area	$\hat{N}$[a]	method	reference
Switzerland, Zurich	330±90	A[b]	Blankenhorn et al. (1969)
	415±14	A[b]	
Switzerland, canton of Zurich	500-1000	E	Escher (1972)
United Kingdom, Oxfordshire	93±36	A[b]	Bell (1979)
	30	B	
Sweden, Gothenburg	342±84[c]	A	Hagström (1979)
France, Bourbon	482±78	A	Zuiderwijk (1980)
Germany, Westphalia	20-40	A[b]	Feldman (1981)
Germany, Münsterland	>60	C[b]	
France, Mayenne	462±129	A	Schoorl & Zuiderwijk (1981)
Germany, Münsterland	101±15[c]	A	Glandt (1982)
	1	B	
	3	B	
United Kingdom, Bucks.	c. 140±13	A	Verrell & Halliday (1985)
United Kingdom, nr. Huntingdon	264±123	A	Cooke (1985)
	56±31	A	
France, Mayenne	40±5	A	Bouton (1986, pers. comm.)
	85±20	A	
	440±100	A	
France, Mayenne	126±21	A	Zuiderwijk & Sparreboom (1986)
Germany, Northrhine-Westphalia	111±8	A	Sinsch (1988)
England, Sussex	102	C,D	Beebee (1990)
Sweden, Öland	172±26[c]	A	Hedlund (1990)
	<30	B?	
	75	B?	
	400	B?	

TABLE 7. Published population size estimates ($\hat{N}$) for *Triturus cristatus*. Methods: A, capture-recapture; B, true census, exhaustive search; C, pond draining; D, funnel traps; E, unspecified. *Notes*: a, SE as published (in some papers SD is given instead of SE) or estimated from population data; b, juveniles not explicitly excluded; c, average over 4-6 consecutive yrs.

be replaced by unrecorded ones. Moreover, it could be argued that a sub-cohort of juveniles exists that escaped detection entirely, because of a fully terrestrial mode of life. If so, the real size of the juvenile population may well have been underestimated. The proportion made up by the terrestrial group is unknown, but it could be substantial. The observation that all juveniles recaptured at age 2 are recruits to the breeding population does not necessarily mean that *all* specimens of that age have sexually matured. What the data do tell us, though, is that if age 2 immatures existed, they were not aquatic but terrestrial.

Fig. 2 suggests that in 1980 about 50% of the newts had not reached adult size at the end of the second and start of the third year, and that only juveniles relatively successful in their phase of somatic growth matured at age 2. This is in line with Smith (1954) who stated that in optimum conditions, crested newts mature at age 2, more commonly at age 3, or at age 4 if the conditions are adverse. In Scandinavia maturation is also recorded at age 2 or 3 but in poor upland habitats they may not breed until they are at least four years of age (Dolmen, 1983*a*). Francillon-Vieillot *et al.* (1990) studying skeletal growth rings in a population of crested newts in central-western France, observed that a certain pattern of growth rings, which they associated with the onset of maturation, was present in newts of age 2 in 11 out of the 23 newts (48%) in which the pattern was observed; the remainder showed this feature at age 3 (48%) or at age 4 (4%). Accordingly, about half of the juvenile population of 1980 will have been breeding in 1981 for the first time, and almost all of the survivors will have been breeding by 1982. Similarly, the efts of 1980, forming the juvenile cohort of 1981 ($\hat{N}$ = 126) will have contributed to the adult population size of 1982 and 1983 (Fig. 4). Assuming, for the sake of argument, a high yearly survival rate as for the adults (S = 49%), the cohort of 1979 estimated at 309 juveniles in 1980, would be reduced to approximately 150 in 1981 and to 75 by then fully mature specimens in 1982. The new cohort of 1980, estimated at 126 juveniles in 1981, would have contributed a further 60 specimens of which about half would have matured, giving a total explained population increase of about 100 specimens. Clearly, this does not fully explain the observed adult population size increase from 1981 and 1982 ($\Delta\hat{N}$ = 177). To account for the difference, we once more are forced to conclude that by restricting observations to the aquatic specimens the size of the juvenile population is underestimated.

The largest and the second largest juvenile cohorts observed were those of 1980 ($\hat{N}$ = 309) and 1981 ($\hat{N}$ = 126). These cohorts gave rise to the biggest observed adult population of $\hat{N}$ = 335 in 1982, for which in terms of reproduction, the basis was led in 1979. This was the year after the first adult crested newts were observed and only two years after the pond had been enlarged.

The estimated annual survival rate for adults was around 49%. This is at the lower end of the range of published data (Table 6), when we exclude Frazer's (1983) estimate for which methodology and data are not specified. Juvenile survival is more variable (Table 4) and larval survival, as indicated by juvenile recruitment, is simply erratic. We conclude that variation in the adult population among years was largely due to variation at those earlier life stages.

Absence of newts from the breeding population that could not be attributed to mortality was noted by Hagström (1979). With a sampling efficiency of averaging at 47%, this observation is of limited value since the large majority of gaps in the records can be explained by census oversights. With a sampling efficiency close to 100%, Hedlund's (1990) data are more informative. Over three different years she estimated the frequency of newts skipping breeding opportunities to average 14% (range 6% to 22%). We have found no such indications but admittedly, as in Hagström's study, sampling efficiency was inadequate to signify absence of newts at that level (see Gill, 1985, 1987; Nichols *et al*., 1987).

With the data at hand a preliminary life table can be drawn up for *T. cristatus*. The fecundity part of the life table has been determined from dissection of females. Approximately 200 eggs are laid by an average adult female each year (published estimates range from 189 to 220 : Hagström, 1980*b*; Arntzen & Hedlund, 1990; Hedlund 1990). Due to a highly unusual chromosome syndrome, 50% of the developing embryos die off at tail-bud stage (Macgregor & Horner, 1980). Mortality of the embryos in the field has not yet been studied as the eggs are deposited singly on aquatic vegetation all over the pond, but loss is bound to be substantial due to predation and oophagy (see below) and drying out of ponds. No data are available on the survival rate of larvae. In a Swedish population, Hedlund (1990) was able to estimate that out of all offspring 0.5% were recruited to the breeding population. With S_j at 22% it can be estimated by interpolation that, out of a single batch of eggs, on the average four to five larvae survive up to and including metamorphosis. This must be considered a minimum estimate because the survival rate for efts is likely to be lower than that for juveniles and two years (occasionally three years) may be required for an eft to become sexually mature (Francillon-Vieillot *et al*., 1989; Arntzen & Hedlund, 1990). With S_a at 50% and one pair of newts per year giving rise to effectively a single adult, a net reproductive rate of unity is just maintained.

Of the twenty-six populations estimated for size that we could find in the literature (Table 7) eight are of equal size or larger than the quarry population in 1982. This overall picture, however, almost certainly is strongly biased towards the larger populations, that were singled out for the purpose of study. Indeed, to quantify a small population by capture-recapture, the most popular and most reliable method, is relatively labour intensive. Glandt (1982) and Sinsch (1988) remarked that some of the populations they studied were among the largest ones in the district. In typical crested newt ponds in Westphalia, Germany, population size was in the order of 20-40 individuals (Feldmann, 1981) and in only 3 out of 230 (1.3%) crested newt breeding sites was the observed number over a hundred. According to Bell (1979) the average population size of the crested newt is 10-20 individuals of reproductive age. Irregular inspection of the study pond and two newly created dune slacks in the remodelled quarry since 1984, including a capture-recapture study in 1992, indicated that the population of crested newts is more or less stable at 20-60 adult individuals.

In the five years following the colonization of the quarry the crested newt developed a sizable population that subsequently collapsed to approximately modal size. No definition seems to be generally agreed upon when to call a colonization 'successful'. As in the case of man-mediated translocations, for such a claim the burden of proof is on the investigator (Dodd & Seigel, 1991) and we echo the call for long term monitoring to ascertain 'success'. With the survival of the newly established population at approximately modal size for a time span exceeding five times the minimum generation time of the species, the colonization of the quarry by the crested newt undoubtedly can be considered a success.

Few studies are long term. A population of crested newts studied by Glandt (1982) over four consecutive years was remarkably stable ($\hat{N}$ ranging from 89-108). On the other hand, in two populations that were studied over a six year period a substantial year to year fluctuation in size was observed where $\hat{N}$ ranged from 150-223 (Hedlund, 1990) and from 230 to 500 (Hagström, 1979), but the observed decline of the quarry population from 1983 to 1984 seems unprecedented. Two aspects of the decline require particular discussion : (i) the low recruitment in the population from the early eighties onwards, and (ii) the very low adult survival from 1983 to 1984. Considering the decline of the population from 1983 to 1984 it cannot be excluded that newts have been collected from the pond for purposes of research or trade. As we have shown, the sampling efficiency can be high in the shallow part of the pond. Another, perhaps more likely possibility is that adult newts died in their terrestrial habitat in the summer and autumn of 1983, being buried when the quarry was remodelled in an attempt to restore the quarry to the original dune habitat.

Considering the lack of recruitment, intensive predation on the pre-metamorphosis stages seems the most plausible explanation. The most sizable animal species in the pond apart from adult crested newts were three-spined sticklebacks (*Gasterosteus aculeatus*), introduced into the quarry pond in 1981. They feed on a wide variety of items (Wootton, 1976), including fish eggs and fish larvae and - presumably - crested newt eggs and hatchlings as well. Only indirect evidence is available suggesting a detrimental effects of the presence of fish on the occurrence of crested newts (Escher, 1972; Clausnitzer, 1983). A strong negative correlation between the presence of fish and the crested newt was found by Beebee (1985). 'Sticklebacks' as predators are named by Bell (1979) and Dolmen (1982), and ten-spined sticklebacks (*Pungitus pungitus*) by Cooke *et al*. (1980). Other potential predators on amphibian larvae in the quarry are the larvae of the dragonflies *Aeshna* sp., *Ischnura elegans* and *Libellula depressa* (Pritchard, 1965; Thompson, 1978; Askew, 1988).

The observed pattern of population development (Fig. 4) with no or little recruitment when adult number peaks suggests intraspecific density-dependent regulation of population size. A substantial spatial and temporal niche segregation is observed between the larval and adult stages of the crested newt (Griffiths & Mylotte, 1987; Dolmen, 1983*b*) suggesting that cannibalism is reduced, but, as in other studies (Crump, 1992), no estimates are available that quantify the effects of cannibalism on the level of the population. Occasional observations were made on crested newts (*T. cristatus*) adult and larvae, respectively, consuming the adults and larvae of smaller newt species (Hagström, 1971; Dolmen & Koksvik, 1983; Frazer, 1983). Inter- and intra-specific oophagy were reported by Avery (1986) and Arntzen (1988), respectively. The occurrence of cannibalism is also reported in some closely related species, without information on the life stages involved (Terent'ev & Chernov, 1949) for *T. karelini*, or by adults on larvae in *T. dobrogicus* (Lac, 1957). In each of the other extensive studies on newt foraging, however, indications of cannibalism (excluding oophagy) are absent (Kühlhorn, 1959; Avery, 1968; Bruno, 1973; Pellantova, 1973; Diaz-Paniagua, 1980; Dolmen & Koksvik, 1983; Stoch & Dolce, 1985; Griffiths, 1986; Griffiths & Mylotte, 1987; Kuzmin, 1991). The fluctuations in the study population may not be controlled by predation and anthropogenic disturbances alone and our interpretation of the data has to be taken with reservation. Drought and other factors may also influence the dynamics of amphibian populations (Berven, 1990). In a long-term study in the southeastern United States juvenile recruitment in particular could be associated to drought, with pond drying being largely responsible for recruitment failures (Semlitsch, 1987; Pechmann *et al.*, 1989; 1991).

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