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High aquatic niche overlap in the newts *Triturus cristatus* and *T. marmoratus* (Amphibia, Urodela)

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Abstract

We studied spatial niche metrics of large-bodied newts (*Triturus cristatus* and *T. marmoratus*) in three breeding ponds in western France. Adults and larvae were sampled with underwater funnel traps. Larvae were identified to the species with diagnostic microsatellite DNA markers. The distribution of adult *T. cristatus* and *T. marmoratus* across pond regions differed in one out of six cases, no differences were observed between larvae (two ponds studied). Niche overlap and niche breadth indices across resource states defined as pond regions or individual traps were high (Schoener's *C*: pond regions 0.60–0.98, traps 0.35–0.71; Levins' *B*: pond regions 0.71–0.98, traps 0.35–0.76). Adults of large-bodied newts significantly differed in resource use from small-bodied newts (*T. helveticus*). The results are discussed in view of the occurrence of interspecific breeding attempts, and the unpredictable ecological characteristics of newt breeding ponds.

Introduction

Amphibians aggregate in limited space when reproducing in standing water. Complex interactions between competition, predation and environmental stochasticity dictate the aquatic community structure (e.g. Wilbur, 1980). In Europe, up to five newt species (urodeles of the genus *Triturus*) share breeding ponds (Arntzen & De Wijer, 1989). Larval and adult guilds of species that differ in size are spatially structured, presumably reducing predation and competition for food (Szymura, 1974; Dolmen, 1983; Griffiths & Mylotte, 1987; Joly & Giacoma, 1992; Fasola, 1993; Braz & Joly, 1994; Miaud, 1996). However, Griffiths (1987) documented highly overlapping spatial niches of adults of the two small-bodied species *Triturus helveticus* (Razoumowski, 1789) and *T. vulgaris* (Linnaeus, 1758), and argued that the unsaturated availability of aquatic resources is the most likely reason for high aquatic niche overlap, with population regulation possibly acting at the larval stage.

Within a contact zone in western France, the large-bodied newts *T. cristatus* (Laurenti, 1768, the crested newt) and *T. marmoratus* (Latreille, 1800, the marbled newt) prefer different landscape types (Schoorl & Zuiderwijk, 1981; Arntzen & Wallis, 1991), but around shared breeding ponds the species showed similar terrestrial habitat utilisation patterns (Jehle & Arntzen, 2000; Jehle, in press). The question of whether these newts differ in their aquatic niche metrics as adults and larvae remains to be studied. Unfortunately, larvae of similar sized and closely related newt species are mostly indistinguishable in the field, and the analysis of ecological niches has so far been hampered by the necessity to sacrifice individuals for biochemical species identification (Arntzen, 1989; De Wijer, 1990). The aims of the present study are to (1) measure niche breadth and overlap in adult *T. cristatus*

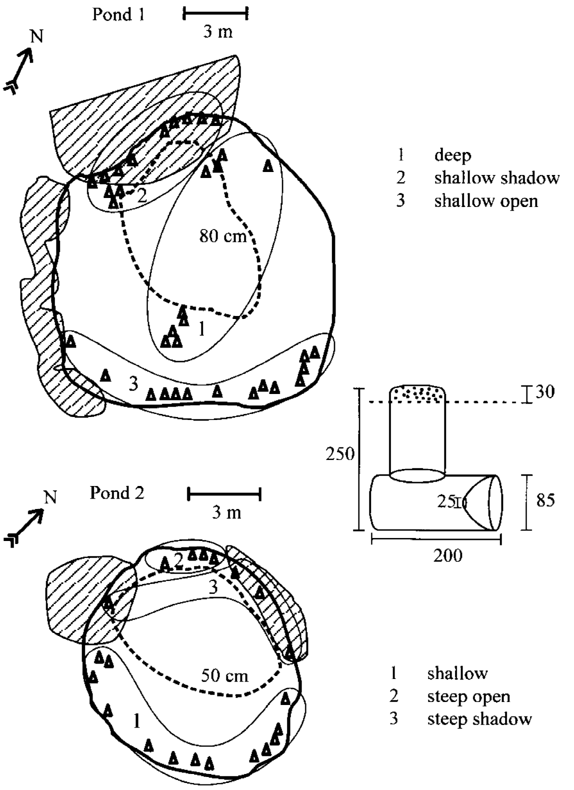

Figure 1. Schematic presentation of Ponds 1 and 2 in 1989 with illustration of trap type used (measures in mm), the number and location of traps (triangles), and resource states defined by pond regions. Pond depth (cm) refers to the water level in spring. Hatching represents trees and bushes.

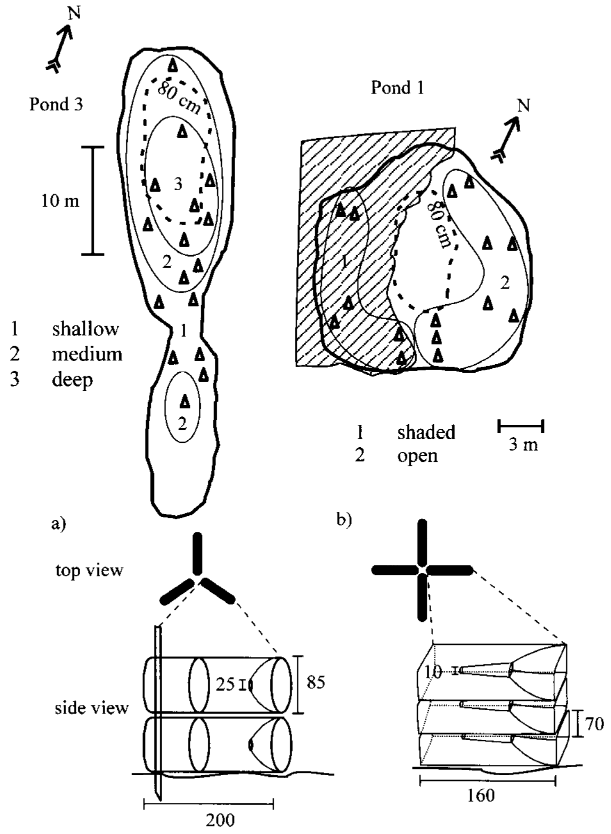

Figure 2. Schematic presentation of Pond 1 in 1998 and Pond 3 in 1997 with illustration of trap types (measures in mm) used for (a) adults and (b) larvae, the number and location of trap units (triangles), and resource states defined by pond regions. Pond depths (cm) refer to the water levels in spring. Hatching represents trees and bushes.

and *T. marmoratus* in three study ponds sampled over a time interval of up to 9 years, (2) measure niche breadth and overlap in larval *T. cristatus* and *T. marmoratus* identified without sacrifice using diagnostic microsatellite DNA markers, (3) compare the niche dimensions of the large-bodied newts *T. cristatus* and *T. marmoratus* with the syntopically occurring small-bodied newt *T. helveticus*.

Materials and methods

Study sites and field work

The three study sites (Figures 1 and 2) are cattle ponds situated in the 'Département' Mayenne, western France. Pond 1 has an area of ca. 200 m^2, Pond 2 has an area of ca. 80 m^2 and Pond 3 has an area of ca. 250 m^2. The surroundings of Pond 1 and Pond 3 are described in Jehle & Arntzen (2000) and Jehle (in press). Adult and larval newts were captured using underwater funnel traps made of plastic bottles (modified after Griffiths, 1985). For adult newts, 2 l bottles with air holes were placed 20 cm deep in the water column (1989), or 1.5 l bottles with no air holes were applied and six bottles formed one sampling unit (1998). For larval newts, square-shaped 1 l bottles were used furnished with an additional funnel to narrow the entrance. Either four traps formed one sampling unit, or 3×4 bottles were vertically packed, allowing to compare captures at the pond bottom with captures in upper pond layers. The pond depths where sampling units were fixed were between 20 cm and 75 cm in Pond 1 and between 20 cm and 100 cm in Pond 3. Figures 1 and 2 illustrate the design, numbers and positions of the funnel traps.

Data on adult newts were collected in Pond 1 between May 23 and June 21 1989 and between April

16 and 25 1998, in Pond 2 over 30 days between April 27 and June 19 1989, and in Pond 3 between April 19 and April 25 1998. Pond 1 was over the 9-year period between observations not exposed to major maintenance, such as dredging. Larvae were captured in Pond 1 between July 7 and August 2 1998 and in Pond 3 at July 20, 21 and 23 1997. Trap locations for capturing adults and larvae were identical. In 1989, traps were inspected around 1000h and 2100h. During spells of hot weather, an additional check was made at around 1400h, but captures were counted as belonging to the evening catch. In 1998, traps for adults were inspected around 0900h and 1900h. Traps for larvae were inspected at around 0800h, 1600h and 2100h in Pond 1 and at 13 4-hour intervals in Pond 3. Adult individuals were group marked by toe clipping and population size estimates were obtained using a weighted mean method (Begon, 1979), with each inspection of traps treated as a sampling session.

In 1989, spatial resource states according to pond regions were defined as follows: ‘shallow open’, ‘shallow shadow’ and ‘deep’ for Pond 1, and ‘shallow’, ‘steep open’ and ‘steep shadow’ for Pond 2 (Figure 1). In 1998, for Pond 1 only two resource states were defined, as the pond had become more overgrown (‘shadow’ and ‘open’) (Figure 2). Pond 3 had a rather uniform shoreline, and resource states were defined according to trap depth (‘shallow’: < 25 cm, ‘medium’: 25–35 cm, and ‘deep’: > 35 cm). In an alternative analysis, each of the sampling units in Ponds 2 and 3 was regarded as an individual resource state; traps which captured no newts were excluded and sexes were pooled due to small sample size. A definition of resource states according to submerged vegetation proved problematic due to the rapid growth of water plants. Ten out of 35 traps in Pond 1 (1989) and three out of 22 traps in Pond 2 (1989) were not always operational, lowering but probably not biasing the capture results. Species-specific differences in capture numbers across pond regions were tested using the *G*-test for independence; such an analysis could not be done for individual traps, as some failed to capture individuals of at least one species. Hybrid newts were excluded from analysis because of small sample size (adults: $n = 10$ in Pond 1 (1989), 10 in Pond 1 (1998), two in Pond 2 and nine in Pond 3; larvae: $n = 9$ in Pond 1 and $n = 1$ in Pond 3). For data obtained in 1989, large-bodied adult newts *T. cristatus* and *T. marmoratus* registered in different pond regions were pooled and compared with captures of the small-bodied *T. helveticus*. Sample size precluded such an analysis in other years and for *T. helveticus* larvae.

Identification of larval newts

One upper gill was removed from captured larvae and immediately stored in 96% ethanol. Effects of gill removal on larval survival and performance were not quantified but 20 larvae kept in an aquarium for 10 days did not show any ill effects. Six percent of the larval catch ($n = 12$) was found dead in the bottle traps and 2% ($n = 4$) died during handling. DNA extractions were performed using standard phenol-chloroform procedures (Sambrook et al., 1989). Larvae were identified to the species with microsatellite primer NT14, larvae collected in 1998 were also identified with primer NT42 (Krupa et al., submitted). PCR products were run on denaturing polyacrylamide gels and either stained with silver nitrate following the Promega Silver SequenceTM DNA sequencing protocol (for NT14), or analysed on an automated ABI 377 DNA sequencer using fluorochrome HEX, standard Tamra 2500, and ABI GeneScan software (for NT42). NT14 produces bands representing alleles of species-diagnostic length. NT42 reveals several alleles with a length of around 490 bp in *T. cristatus* and several alleles of around 170 bp in *T. marmoratus*. In 6% of the larval tissue samples, the PCR amplification of DNA failed. The remaining samples could be unequivocally identified.

Niche breadth and niche overlap

Niche breadths were calculated using index *B* (Levins, 1968):

$$B = 1/(n\Sigma \mathrm{p}^2 xi),$$

in which p_{xi} is the proportion of species x using resource i, and n is the number of resources available. B ranges from $1/n$ (use of a single resource) to 1 (equal usage of resources). Niche overlap was calculated using the index *C* (Schoener, 1970):

$$C = 1 - 0.5(\Sigma \mid \mathrm{p}_{xi}\mathrm{p}_{yi} \mid),$$

in which p_x and p_y are the proportions of species x and y captured using resource i. C ranges from 0 (no overlap) to 1 (full overlap). These are the same indices as applied by Griffiths (1987) in his study on syntopic *T. helveticus* and *T. vulgaris*. Different numbers of traps/trap units per pond region, however, precluded the calculation of sampling variates for niche indices and subsequent tests for differences among groups.

Table 1. Captures of the newts *Triturus cristatus* and *T. marmoratus* in syntopic breeding ponds in western France. Adult population size was estimated with a weighted mean method from capture-recapture data (Begon, 1979)

	Study year	Females	Males	Larvae	Adult population size ± SE
T. cristatus					
Pond 1	1989	34	11	–	76.5 ± 25.6
	1998	17	26	25	73.0 ± 18.9
Pond 2	1989	14	28	–	17.5 ± 3.6
Pond 3	1997	–	–	118	–
	1998	142	142	–	585.6 ± 78.3
T. marmoratus					
Pond 1	1989	38	16	–	146.0 ± 55.4
	1998	9	47	48	147.4 ± 28.4
Pond 2	1989	172	99	–	252.7 ± 24.4
Pond 3	1997	–	–	17	–
	1998	9	22	–	57.0 ± 32.6

Results

Adult newts

Four hundred and fourteen adult *T. cristatus* and 412 adult *T. marmoratus* were registered. Newts were caught in almost all sampled parts of the ponds, but the number of captures per trap or trap unit varied greatly. Ranges in capture rates were from zero to 13 (1989), and from zero to 17 (1998) in Pond 1, from one to 32 in Pond 2 and from five to 34 in Pond 3. Adult population size was 205.9 ± 50.0 in Pond 1 (1989), 210.6 ± 31.1 in Pond 1 (1998), 261.6 ± 22.9 in Pond 2 and 656.9 ± 84.4 in Pond 3. The contribution of *T. cristatus* was 33%, 33%, 7% and 91%, respectively (Table 1).

A significant difference was observed between males and females of *T. cristatus* in Pond 3, with males predominating in lower and females in upper layers of the pond ($G = 7.08$, d.f. = 1, $p < 0.01$). No such differences were observed between the sexes for *T. marmoratus* ($G = 0.02$, d.f. = 1, $p > 0.05$), or in Pond 1 (*T. cristatus*: $G = 0.00$, d.f. = 1, *T. marmoratus*: $G = 0.51$, d.f. = 1, $p > 0.05$). Comparison of captures from the pond bottom and upper layers yielded significant interspecific differences for Pond 1 ($G = 8.29$, d.f. = 1, $p < 0.01$) and Pond 3 ($G = 6.79$, d.f. = 1, $p < 0.01$). *Triturus cristatus* was predominant in lower traps in Pond 1 and in upper traps in Pond 3. No significant difference between the species was observed in daytime captures versus nighttime captures (Pond 1, 1989: $G = 2.67$, Pond 2: $G = 0.79$, $p > 0.05$). For adults captured in Ponds 1 and 2 in 1989, with data available over a relatively long time span, no indication was found for seasonal differences in habitat niche occupation (three sampling periods of equal length: Pond 1, $G = 2.25$, d.f. = 2; Pond 2, $G = 2.98$, d.f. = 2, $p > 0.05$).

From the six pond-study year combinations, the distribution of *T. cristatus* and *T. marmoratus* captured in different pond regions was significantly different for Pond 1 in 1989 ($G = 13.29$, d.f. = 2, $p < 0.01$), but in other ponds and sampling years the distributions were indistinguishable. Niche breadth indices were between 0.53 and 0.93 for *T. cristatus* and between 0.35 and 0.98 for *T. marmoratus* (Table 2). Overlap indices between *T. cristatus* and *T. marmoratus* ranged from 0.35 to 0.93. Males and females had similar overlap indices (Table 2, Wilcoxon sign-rank test: $z = 1.64$, $p > 0.05$). A significant difference in resource use was observed between pooled numbers of large-bodied newts and the small-bodied *T. helveticus* (Pond 1: $G = 11.02$, d.f. = 1, $p < 0.0001$; Pond 2: $G = 72.73$, d.f. = 1, $p < 0.001$). For identical resources, lower niche overlap indices for small- and large-bodied newts were observed than among the large-bodied species (Pond 1, males: $C = 0.67$, females: $C = 0.72$, total: $C = 0.69$; Pond 2, males: $C = 0.74$, females: $C = 0.63$, total: $C = 0.55$).

Larval newts

The contribution of *T. cristatus* to the larval population was 34% (Pond 1, 1998) and 87% (Pond 3, 1998). Significant differences in species composition between adults and larvae were not observed (Pond 1: $G = 1.44$, d.f. = 1; Pond 3: $G = 0.01$, d.f. = 1, $p > 0.05$). No significant differences were observed in captures of *T. cristatus* and *T. marmoratus* larvae in different pond regions (Pond 1: $G = 1.91$, d.f. = 1, Pond 3: $G = 0.07$, d.f. = 2, $p > 0.05$) or between larvae captured on the pond bottom and in the upper layers (Pond 1: $G = 2.26$, d.f. = 2, Pond 3: $G = 1.85$, d.f. = 2, $p > 0.05$). Niche overlap indices in larvae were mostly higher than those for adults in identical resources, niche breadth indices were of the same order (Table 2).

Discussion

This study indicates that the niche overlap between similar-sized newt species is high at both the adult and larval life stage. PCR (Polymerase Chain Reaction)-based mitochondrial DNA and RAPD (Random Amplified Polymorphic DNA) analysis have recently proven to successfully identify newt hybrids (Beebee

Table 2. Niche breadth index (*B*) and niche overlap index (*C*) in syntopic *Triturus cristatus* and *T. marmoratus* in western France. Spatial resources are defined by pond region or by individual traps (see text for details)

		Niche breadth index (*B*)		Niche overlap index (*C*)		
		T. cristatus	*T. marmoratus*	Total	Males	Females
Adults						
Pond 1,	1989 pond regions	0.77	0.71	0.82	0.85	0.60
	Traps	0.53	0.35	0.35	–	–
	1998 pond regions	0.93	0.75	0.92	0.91	0.93
	Traps	0.57	0.53	0.63	–	–
Pond 2,	pond regions	0.81	0.74	0.69	0.78	0.66
	Traps	0.69	0.55	0.57	–	–
Pond 3,	pond regions	0.91	0.98	0.89	0.95	0.82
	Traps	0.48	0.76	0.63	–	–
Larvae						
Pond 1,	pond regions	0.93	0.75	0.84	–	–
	Traps	0.42	0.68	0.67	–	–
Pond 3,	pond regions	0.82	0.84	0.98	–	–
	Traps	0.59	0.49	0.71	–	–

et al., 1999). In the present study, we show that a PCR amplification of nuclear microsatellite loci is a powerful tool to undestructively identify morphologically indistinguishable newt larvae. The lack of consistency in sampling regime precludes precise comparisons in niche metrics between years and ponds, but offers the possibility to explore the niche dimensions on different scales. Treating every trap/sampling unit as a resource state provides a finer-scale analysis, and is offset against the analysis of pond regions. That indices were lower for individual traps/sampling units could be caused by a smaller sample size per resource, increasing stochasticity in the relative species distributions between traps. For the analysis of pond regions, pseudoreplication due to aggregations of newts in specific regions could bias the results, and for the analysis based on single traps spatial autocorrelation due to several sampling units placed in one region might occur. However, as both study species behave similarly both at the finer- and broader-scale analysis, these effects are probably small. The tendency that spatial overlap was smaller for females than for males could be due to interspecific difference in oviposition sites, as observed for size-structured newt guilds (Miaud, 1995). The biological meaning of the different distributions of adult *T. cristatus* and *T. marmoratus* at the pond bottom and in upper layers remains unclear. Within one season, adult *T. cristatus* and *T. marmoratus* differ in their phenology (Bouton, 1986), but differences in their aquatic niches between sampling periods were not observed. Griffiths (1987) observed that habitat niche metrics varied over time in *T. helveticus* and *T. vulgaris*. De Wijer (1990) found no temporal niches difference in larval *T. helveticus* and *T. vulgaris*, but observed that the relative frequency of species changed over time. A similar analysis for *T. cristatus* and *T. marmoratus* could not be performed due to the short annual periods of sampling.

This is the first study that measured niche metrics in a pond over a 9 years interval, and the data indicate that major changes in spatial overlap did not occur over this relatively long time period. Compared to 1998, overlap indices in Pond 1 were slightly smaller in 1989, when the pond was probably at an earlier stage of succession, but it has to be considered that the sampling regimes were not identical. That spatial habitat partitioning of newt larvae can vary between ponds at different successional stages has been previously documented with, however, different effects for various species (Braz & Joly, 1994).

A high niche overlap between adult *T. cristatus* and *T. marmoratus* might contribute to the frequency at which the species hybridise (Arntzen & Wallis, 1991). In turn, indiscriminate sexual behaviour may result in convergent niches, and niche selection resulting from mating behaviour could override existing ecological segregation. Field observations have shown that *T. cristatus* and *T. marmoratus* assemble during courtship (Zuiderwijk, 1990). However, niches of newts registered at dusk and night, when courtship activity is highest, were not different from daytime niches. In *T. vulgaris* and *T. helveticus*, spatial niche overlap was higher than predicted by a randomised neutral model, suggesting ecological convergence rather than divergence (Griffiths, 1987). However, interspecific breeding was not inferred as an explanation, perhaps because successful hybridisation is less frequent in this species pair than in *T. cristatus* and *T. marmoratus* (Griffiths et al., 1987; Arntzen & Wallis, 1991; Arntzen et al., 1998).

A breeding-site survey in Mayenne suggested that *T. cristatus* predominates in large ponds situated in flat and open landscapes and that *T. marmoratus* predominates in small ponds in hilly and forested landscapes (Schoorl & Zuiderwijk, 1981). Tracking terrestrial movements of adults around shared breeding ponds showed, however, that *T. cristatus* and *T. marmoratus* mostly use the same habitats and refuges (Jehle & Arntzen, 2000; Jehle, in press). If a similar ecological pattern exists for aquatic niches, the comparison of niche metrics of allotopic *T. cristatus* and *T. marmoratus* might reveal differences impossible to observe in syntopic populations. In other words, the mechanisms responsible for aquatic niche segregation might act at the between-pond scale rather than within ponds. This would imply ecophysiological constraints rather than the behavioural avoidance of competition, a hypothesis which could be tested by comparing the niche metrics and performance of *T. cristatus* and *T. marmoratus* in a series of ponds naturally inhabited by just one species or the other.

In communities of pond-breeding amphibians, predation and competition interact within the context of a disturbance gradient related to pond hydroperiod (Pechmann et al., 1989; Semlitsch et al., 1996). Notwithstanding the regular loss of entire cohorts of larvae due to pond desiccation, temporary ponds in wet years are especially suitable sites for reproduction because predators are usually less abundant (Griffiths, 1997). This suggests that both density-independent and density-dependent regulation factors play important roles in population regulation. Niche diversification may primarily be driven by density-dependent factors. *Triturus* newts are abundant in the area of investigation (Arntzen & De Wijer, 1989) and high densities preclude diffuse competition due to niche vacancies (Pianka, 1974). The observed niche differentiation between large-bodied and small-bodied newt species was caused by more captures of *T. helveticus* in shallow pond areas. In 1989, the adult population size of *T. helveticus* in Pond 2 was estimated as 1002 newts, i.e. averaging at >12 newts per m^2 (Arntzen et al., 1998). This suggests that the aquatic resources may be limiting, inducing the segregation of spatial niches. Predation and competition for food have been considered as the forces driving such segregation (Dolmen, 1983; Griffiths & Mylotte, 1987; Fasola, 1993). Another possible cause of the observed niche segregation is that females of big- and small-bodied newt species prefer different substrates for oviposition (Miaud, 1995). Spatial differences were not, however, reflected in a lower niche overlap in females than in males. Larvae of *T. cristatus* were found to be more nectontic than adults, which was interpreted as a mechanism limiting cannibalism (Dolmen, 1983). Data collected after hatching of eggs, in combination with stomach flushing of adults, would provide further insights into the role of predation in population regulation.

Typical amphibian breeding sites have highly variable within- and between-year water levels and temperature regimes, and often experience drastic changes due to vegetational successions. Amphibian life-histories are adapted to exploit the uncertainties associated with rapid ecological change. The highest species richness in a gradient of habitats was observed at sites with high temporal variability (Morand & Joly, 1995). A high niche overlap is commonly observed in highly dynamic aquatic ecosystems, and stochastic fluctuations of the environment are associated with a reduced level of exploitation competition (Hutchinson, 1961). Studies on similar-sized newts documenting mostly indiscernible niches (Griffiths, 1986, 1987; De Wijer, 1990; this study) suggest that such mechanisms also act in newt breeding ponds. Alternatively, a high niche overlap may result from an unlimited availability of resources (Griffiths, 1987). Future studies could concentrate on the spatial and feeding niche metrics of adults and larvae under varying densities and food supply, for example in experimentally manipulated ponds. Niche metrics that are stable under varying resource levels would indicate that the low degree of aquatic niche segregation in similar-sized *Triturus* newts reflect the high stochasticity of the aquatic habitat.

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