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Resource partitioning in two heterochronic populations of Greek Alpine newts, *Triturus alpestris veluchiensis*

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Abstract

Current ecological models suggest that the maintenance of trophic polymorphisms is favoured by a different resource use in alternative morphs. Facultative paedomorphosis in newts is an example of phenotypic variation as paedomorphs retain morphological larval traits, such as gills and gill slits. The aim of this study was to find out whether heterochronic morphs occupy particular micro-habitats and focus on specific prey items. Resource partitioning was found between morphs. It concerns mainly food selection with paedomorphs preying more on plankton and less on terrestrial invertebrates than metamorphs. Some habitat specializations were also found with metamorphs being more abundant at the water surface than paedomorphs. Diel variation in habitat use of the two different morphs was minimal. Polymorphism allows Alpine newts to exploit the different resources in the lakes in order to minimize intraspecific competition, but the extent of resource partitioning depends on habitat characteristics.

Keywords *Resource partitioning; Diet; Habitat; Predator-prey relationships; Heterochrony; Paedomorphosis; Polymorphism*

1. Introduction

Resource polymorphisms are defined as the occurrence of discrete intraspecific morphs showing differential niche use Skulason and Smith, 1995 and Smith and Skulason, 1996. They have been found in a wide range of animals, including fishes (Malmquist et al., 1992), amphibians (Collins et al., 1993), and birds (Smith, 1990). A decrease of interspecific competition and the presence of under-exploited niches promote resource polymorphisms Skulason and Smith, 1995 and Smith and Skulason, 1996. Polymorphisms are also suspected to play an important role in species evolution as habitat shift between alternative morphs might be followed by separate differentiation and then sexual isolation West-Eberhard, 1989, Bush, 1994 and Skulason and Smith, 1995.

In newts and salamanders, two resource-based polymorphisms have been identified: cannibalism Collins et al., 1993 and Michimae and Wakahara, 2001 and facultative paedomorphosis Whiteman et al., 1996 and Denoël and Joly, 2001. The two can also be coupled Collins, 1981 and Larson et al., 1999. Cannibalism is expressed not only behaviourally, but also morphologically, with the cannibalistic morphs having large heads and teeth Collins et al., 1993 and Michimae and Wakahara, 2001. Facultative paedomorphosis is a heterochronic process in which larval traits are retained in the adult (Gould, 1977). This means that paedomorphs are reproducing individuals possessing fully developed external gills and open gill slits Semlitsch and Wilbur, 1989, Breuil, 1992, Whiteman, 1994 and Denoël et al., 2001b. By retaining a larval morphology, paedomorphs exhibit a feeding system different from that of metamorphs. Paedomorphs suck prey into the mouth and expel water between the gill bars while metamorphs are constrained to evacuate water through the mouth Joly, 1981 and Lauder and Shaffer, 1993. This morphological variation between morphs results in different success rates of capture, with paedomorphs being more efficient in foraging on planktonic organisms, while aquatic metamorphs have higher success rates in capturing terrestrial invertebrates that fall on the water surface Whiteman et al., 1996 and Denoël, 2001.

Resource use has been poorly studied in alternative heterochronic morphs of tailed amphibians coexisting in the same aquatic habitat. In a deep French alpine lake, results are consistent with the difference in feeding success observed between morphs (Denoël, 2001): paedomorphs focused on plankton and aquatic metamorphs on terrestrial insects (Denoël and Joly, 2001). Morphs also segregate according to micro-habitat: paedomorphs inhabited all sectors of the lake, whereas metamorphs were limited to peripheral areas (Denoël and Joly, 2001). Resource partitioning was also found in small Italian ponds, but was less pronounced Fasola and Canova, 1992, Fasola, 1993 and Denoël, 2001. Spatio-temporal variability in a heterogeneous habitat and the relations between space use by newts and their prey have not yet been explored in paedomorphic newt populations.

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The aim of this study was to determine differences in resource use of paedomorphic and metamorphic Greek Alpine newts (*Triturus alpestris veluchiensis*) in two deep high-altitude lakes. We focused on food and space variation between morphs, and on the spatio-temporal distribution of newts and their pelagic prey. We expected resource partitioning in the two lakes, with some differences in the two populations according to the characteristics of the lakes (heterogeneity).

2. Materials and methods

2.1. Species description and study sites

The Alpine newt is an amphibian species widely distributed in Europe. In most populations, the aquatic larvae transform into metamorphosed juveniles, which reach maturity on land, but facultative paedomorphosis has been recorded in at least 87 sites, mainly in the Italian and Balkan peninsulas (Denoël et al., 2001). The largest dimorphic populations inhabit alpine lakes of Montenegro, Albania and Greece (Denoël, 2001). The two morphs can easily be distinguished by the presence of gills and gill slits in the paedomorphs. Sexes can also be distinguished because the cloaca of males is smooth and swollen, whereas in females, it is thin, elongated and striated (Denoël et al., 2001).

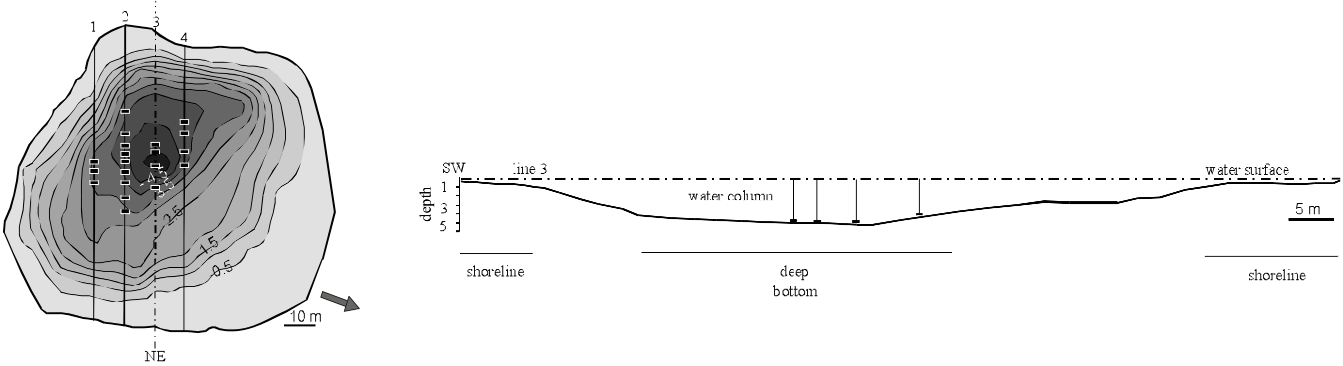
We studied two populations of the Greek Alpine newt *Triturus alpestris veluchiensis* (Wolterstorff, 1935) living in fishless alpine lakes. The two aquatic sites are located in Ioannina district, Epirus, North-West Greece, and are both named “Drakolimni”, which means “Dragon Lake”. One is located in the Tymphi Mountains (39°59’N, 20°47’E, 2000 m elevation) and the other in the Smolikas mountains (40°05’N, 20°54’E, 2140 m elevation). These two sites will be referred to as “Tymphi” and “Smolikas”. No exchange exists between the two lakes because an impassable deep valley separates them. Fieldwork was conducted between 14 and 22 July 1999 at Smolikas and between 29 July and 3 August 1999 at Tymphi.

The lakes are surrounded by alpine pasture. We determined bathymetry by sounding the depths along parallel transects across the lakes. Tymphi has a somewhat quadratic appearance. The maximum diameter, volume, and maximum depth are 100 m, 16,000 m3 and 4.95 m, respectively (Fig. 1a). Vegetation is abundant near the shoreline and consists mostly of *Carex* sp. A few yellow-bellied toads (*Bombina variegata scabra*) and green toads (*Bufo viridis viridis*) inhabited the lake. Smolikas is more rectangular. It is 122 m long, 61 m wide and has a maximum depth of 3.7 m and a volume of 6000 m3 (Fig. 1b). Vegetation (*Carex* sp.) is limited to small shallow patches. The bottom is muddy and rocks are rare. Smolikas thus differs from Tymphi in being more homogeneous. Two Macedonian crested newts (*Triturus carnifex macedonicus*) and three green toads have been observed in the Smolikas lake.

2.2. Sampling and analysis

Several different sampling methods were used. Newts were caught by dip-netting from the shore or from a boat, by snorkelling and by trapping. Trap design was described in detail by Griffiths (1985). Briefly, our system consisted of a 1.5 l plastic bottle from which the bottom was removed and replaced by the neck of another bottle with the open cap pointing toward the interior of the bottle. A cap closed the exterior neck to retain the caught newts in the bottle. The traps were placed horizontally in the water column and a metal plate on the bottom

A. Tymphi



B. Smolikas

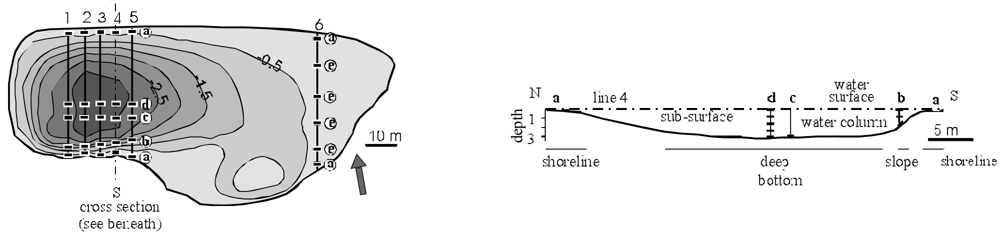


Figure 1 Bathymetric maps (left) and cross-sections (right) of Drakolimni from Tymphi (A) and Smolikas (B). The positions of traps are shown by black boxes along trapping lines. The cross-section corresponds to lines 3 and 4 in Tymphi and Smolikas, respectively. The extension of the different sampling strata is indicated. The depth range is presented in the text. The arrows indicate the north.

assured a levelled and stable position. The traps were stringed on vertical cords in pre-determined distances from the water surface (Fig. 1) with 1–5 traps on each vertical line. This allowed us to catch newts on the bottom and in the open water.

In Tymphi, the five main micro-habitats were investigated (Fig. 1a): “bottom of the shoreline without vegetation” (0–0.7 m depth), “bottom of the shoreline with vegetation” (0–0.7 m depth), “water surface in vegetated areas”, “open water column” (0.5–2 m depth) and “deep bottom of the lake” (3.2–4.9 m depth). Newts were caught by dip-netting in the first four micro-habitats and with traps in the deep parts (20 bottles positioned on four transects crossing the deep area of the lake; Fig. 1a).

At Smolikas, six major micro-habitats were sampled (Fig. 1b): “bottom of the shoreline” (0–0.5 m depth), “bottom of the slopes” (1.4–1.6 m depth), “deep bottom” (2.7–3.95 m depth), “open water column” (0.5–2.4 m depth), “sub-surface” in the central part of the lake (0–0.05 m depth), and “water surface” close to the shoreline (0 m depth). Free-floating newts were only caught right at the water surface. Newts caught in the sub-surface habitats were swimming in the upper water column, ascending to the water-surface only to breathe. Newts were collected with nets and traps in the deep bottom, water column and shore bottom, but only with traps at the sub-surface and slope bottom. Dip-netting was used to catch animals at the water surface. Traps were exposed along six transect lines crossing the lake (five lines crossing the deep area and one crossing the shallow area; Fig. 1b). They were fixed in an identical manner in the first five horizontal lines. On each of these five lines, there were two traps right at the bottom of the deep area, two at the bottom of the shoreline, one at the bottom of the slope area and six in the open water column (in the slope area: one trap at 0.8 m depth and one just beneath the water surface; in the central area: one trap at 2.4, 1.6, and 0.8 m depth each, and one just under the water surface; Fig. 1b). Ten traps were also placed on a line crossing the shallow area of the lake with six traps at the bottom and four just under the water surface (Fig. 1b). The traps were checked every 4 h over a 72-h period (sampling at 1 a.m., 5 a.m., 9 a.m., 1 p.m., 5 p.m., and 9 p.m., local time; sampling time: 1 h). In between checking our traps, we also sampled *Daphnia* sp. and *Chaoborus* sp.; two pelagic prey items of the Alpine newt. Every 4 h, samples were taken with a 5 l Schindler trap over a 24-h period (at 3 a.m., 7 a.m., 11 a.m., 3 p.m., 7 p.m., and 11 p.m.). The density of these primary prey items was determined at the deepest point of the lake and at the same depth intervals as those used for the traps.

The total population size and 95% confidence limits (shown in brackets) were estimated by means of a capture-mark-release-recapture procedure, using the Petersen index (Greenwood, 1996). Newts were kept in containers filled with water from the lake until the end of the whole sampling period to avoid recapture; however, marked individuals were released right after marking. Animals were marked by tattooing an Alcyan blue spot on the middle of the ventral side (Joly and Miaud, 1989).

Immediately after capture, we anaesthetized the newts (0.5% phenoxyethanol solution) and extracted their stomach contents using a stomach flushing technique described by Joly (1987). To avoid prey digestion after capture (Schabetsberger, 1994), newts used in the stomach content study were caught by dip-netting and not by trapping. However, we used trapped newts of the deep bottom at Tymphi, but we only flushed individuals that had remained less than 3 h in the trap. The stomach contents were individually stored in vials and preserved in 4% formaldehyde. Prey items were identified using a stereoscopic microscope.

Chi-square tests were used to test the null hypothesis for equal proportions of newts of the two morphs among micro-habitats. Probabilities have been corrected using Bonferroni procedure to take into account multiple comparisons. MANOVAs with Tukey’s post-hoc tests were used to test the null hypothesis for equal number of prey in the stomachs of the two morphs (“square-root + 0.5” transformation). Tukey’s test was chosen to take into account the dependent effect of the different kinds of prey consumed by each newt (Day and Quinn, 1989).

3. Results

3.1. Population size

At Tymphi, as 424 newts were marked at the first sampling occasion and 503 were caught at the second, of which 38 were marked, total population size was estimated to be 5491 (95 % C.I.: 4300-8077) adults, yielding a density of 0.3 (0.3 – 0.5) individuals m^{-3}. Paedomorphs accounted for 34% of the adult population (*n* = 474). At Smolikas, as 1887 newts were marked at the first capture session and 1548 caught at the second, of which 111 were marked, population size was estimated to be 26111 (95 % C.I.: 22331-32032) adults, which yields a density of 4.4 (3.7 – 5.4) individuals m^{-3}. Paedomorphs accounted for 74% of the adult population (*n* = 1887).

3.2. Micro-habitat partitioning

Paedomorphs and metamorphs differed in micro-habitat use at Tymphi ($\chi^2 = 101.7$, 4 df, $P < 0.001$, $n = 571$; Fig. 2). Pair-wise statistical comparisons between habitats and morphs are all significant ($P <$

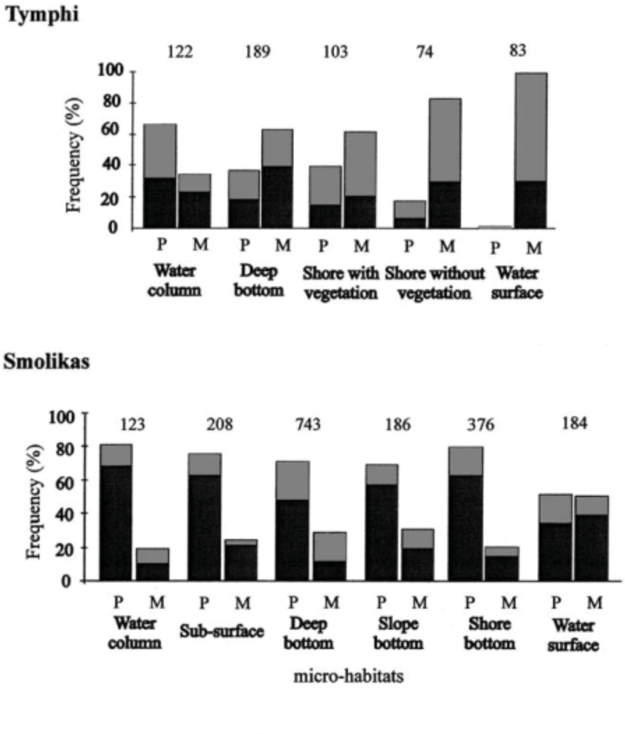


Figure 2. Spatial use of micro-habitats by Alpine newts in Tymphi (up) and Smolikas (down). P: paedomorphs; M: metamorphs; black bars: females; shaded bars: males.

Table I Difference in micro-habitat use between Alpine newt paedomorphs and metamorphs in Tymphi ($\chi 2$-test in 2 × 2 contingency tables). +v, with vegetation, −v, without vegetation (see Fig. 1 for micro-habitat locations). **P*, corrected *P* values according to multiple comparisons

Habitat	$\chi 2$(1 df)	*P*	*P**
Shore (+v) × shore (−v)	9.28	<0.01	<0.01
Shore (+v) × deep bottom	0.15	0.69	1
Shore (+v) × water column	16.04	<0.001	<0.001
Shore (+v) × water surface	37.87	<0.001	<0.001
Shore (−v) × deep bottom	8.89	<0.01	<0.05
Shore (−v) × water column	42.57	<0.001	<0.001
Shore (−v) × water surface	12.9	<0.001	<0.001
Deep bottom × water column	20.26	<0.001	<0.001
Deep bottom × water surface	42.71	<0.001	<0.001
Water column × water surface	85.63	<0.001	<0.001

0.05), except in the habitat "shoreline with vegetation" and «deep bottom» (χ^2 test; Table I). Although metamorphs accounted for two thirds of the population, paedomorphs were two times more abundant in the water column than metamorphs. Unlike metamorphs, paedomorphs were very rarely found at the water surface.

At Smolikas, paedomorphs and metamorphs also differed in micro-habitat use ($\chi^2 = 59.71$, 5 df, $P < 0.001$, $n = 1820$; Fig. 2). At the water surface, metamorphs were as numerous as paedomorphs although they accounted for only one quarter of the population. Frequencies of morphs at the water surface significantly differed from those in each of the other habitats (χ^2 test, $P < 0.01$; Table II). Significant differences in habitat use between morphs were noted on the bottom of the deep and shallow parts of the lake (χ^2 tests, $P < 0.01$; Table II). However, although significant, the difference between the proportions of the two morphs accounted for only 5% (Fig. 2). At the water surface and sub-surface the proportion

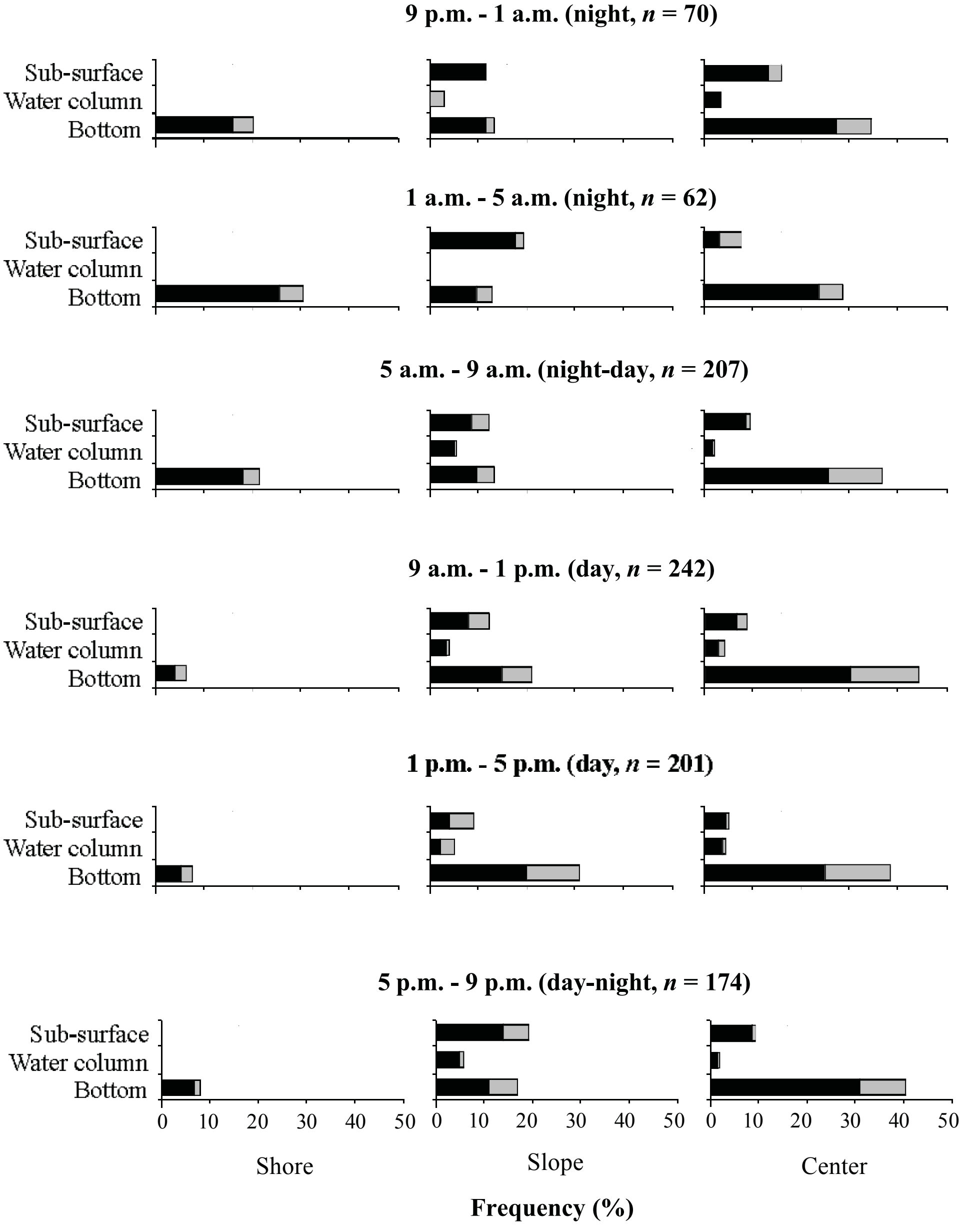


Figure 3 Spatio-temporal use of micro-habitats by Alpine newts in Smolikas. Black bars: paedomorphs; shaded bars: metamorphs. Left: shore area, centre: slope area, right: central area. Micro-habitats: sub-surface, water column, bottom (0.3 m depth in shore area, 1.6 m depth in slope area, 3 m depth in central area). For a given sample time, the addition of the bars at the left, centre and right equal 100%.

Table II Difference in micro-habitat use between Alpine newt paedomorphs and metamorphs in Smolikas ($\chi2$ test in 2 × 2 contingency tables) (see Fig. 1 for micro-habitat locations). **P*, corrected *P* values according to multiple comparisons

Habitat	$\chi2$(1 df)	*P*	*P**
Shore × deep bottom	9.82	<0.01	<0.01
Shore × slope bottom	7.08	<0.01	<0.05
Shore × water column	0.18	0.67	1
Shore × sub-surface	1.28	0.26	1
Shore × water surface	49.4	<0.001	<0.001
Deep bottom × water column	5.82	<0.05	0.08
Deep bottom × sub-surface	1.76	0.18	1
Deep bottom × water surface	27.26	<0.001	<0.001
Deep bottom × slope bottom	0.15	0.70	1
Water column × sub-surface	1.51	0.22	1
Water column × water surface	29.87	<0.001	<0.001
Water column × slope bottom	5.51	<0.05	0.09
Slope bottom × water surface	13.64	<0.001	0.001
Slope bottom × sub-surface	1.85	0.17	0.85
Water surface × sub-surface	26.28	<0.001	<0.001

of the two morphs differed (χ^2 = 26.28, 1 df, $P <$ 0.001). No significant difference was found in the proportion of the two morphs caught by the two methods (dip-netting and trapping) in the other micro-habitats: water column (χ^2 = 2.32, 1 df, P = 0.13), deep bottom (χ^2 = 0.39, 1 df, P = 0.53) and shore bottom (χ^2 = 2.18, 1 df, P = 0.14).

Abundance of newts in the different micro-habitats changed during the diel period at Smolikas (Fig. 3). At night, newts were abundant on the «bottom of the shore-line» but were rare in this area during the day. On the other hand, newt abundance increased during the day on the «bottom of the slope region». Some newts remained in the periphery of the lake during the day where they hid under grass overhanging the shoreline region. This was the only shelter available in the lake, as it is devoid of rocks and also poor in vegetation. Catches were highest during the day, followed by catches during dawn, dusk and during the night. The two morphs did not exhibit opposed distribution patterns throughout the different sampling periods. However, a larger proportion of metamorphs were found at the «deep bottom of the lake» during the day (Fig. 5).

3.3. Food partitioning

At Tymphi, 184 newt stomachs were sampled from 45 female metamorphs, 50 female paedomorphs, 43 male metamorphs, and 46 male paedomorphs. They resulted in the identification of 4834 prey items. Four main prey categories were eaten by the newts: Crustacea (Daphniidae, Chydoridae, Calanoida, Cyclopoida, Ostracoda), aquatic Insecta larvae (Chironomidae, Hemipteroidea, Ephemeroptera, and Dytiscidae), Hydracarina, and terrestrial invertebrates (Diptera, Coleoptera, Hemipteroidea, Hymenoptera, Arachnida). Diet composition differed between morphs in males (MANOVA, $F_{4,84}$ = 6.738, $P <$ 0.001) and females (MANOVA, $F_{4,90}$ = 11.93, $P <$ 0.001). Paedomorphic males preyed significantly more on crustaceans than their metamorphic counterparts (Tukey's test, P < 0.001; Fig.

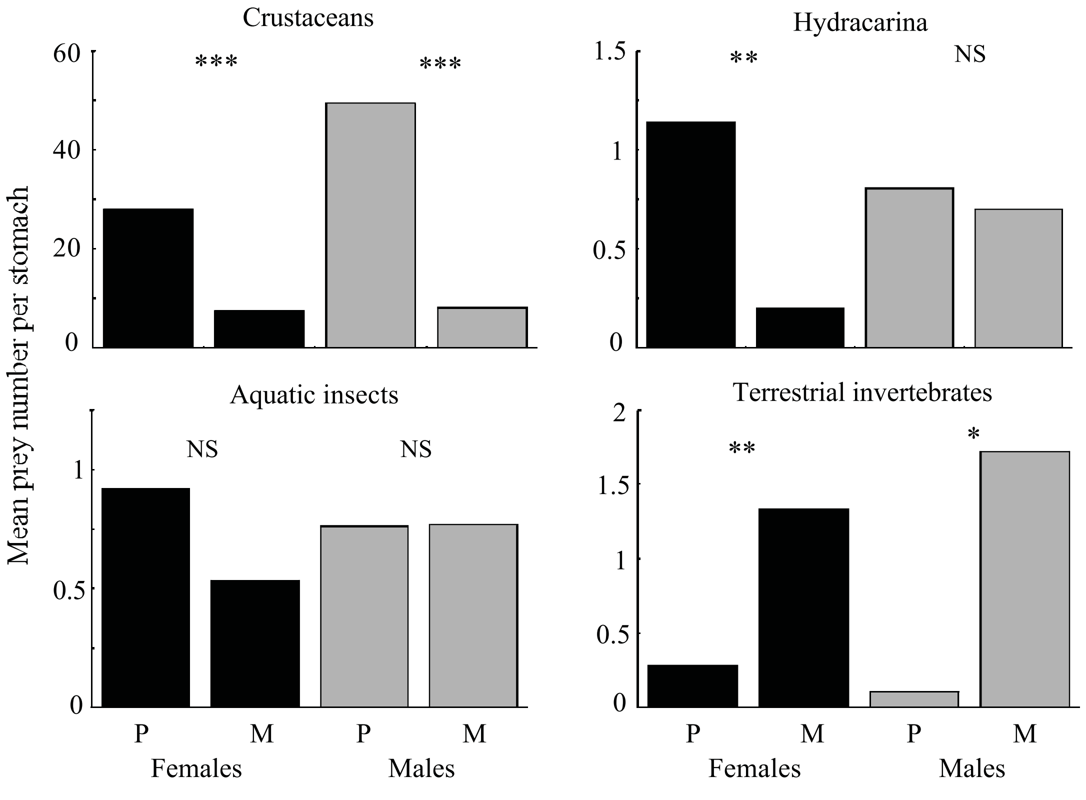


Figure 4. Diet of the Alpine newts in Tymphi. P: paedomorphs; M: metamorphs; black bars: females; shaded bars: males. **P < 0.01, ***P < 0.001, ^{NS} P > 0.05 (MANOVA: Tukey's tests)

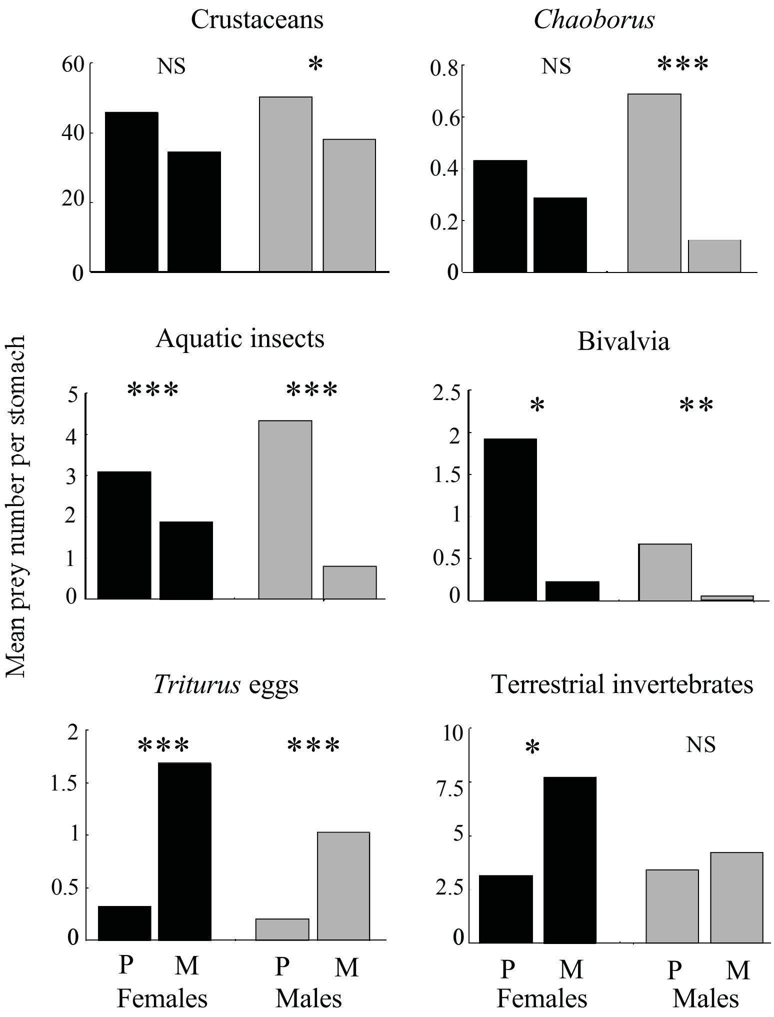


Figure 5. Diet of the Alpine newts in Smolikas. P: paedomorphs; M: metamorphs; black bars: females; shaded bars: males. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, $^{NS}P > 0.05$ (MANOVA: Tukey's tests).

4). The same was observed in females ($P < 0.001$). A significantly larger number of Hydracarina was also found in paedomorphic females ($P < 0.001$) but not in males ($P = 0.95$; Fig. 4). Metamorphic males and females ingested more terrestrial invertebrates than paedomorphs (females: $P < 0.001$, males: $P < 0.01$; Fig. 4). No significant difference between morphs was found for predation on aquatic insect larvae (females: $P = 0.06$; males: $P = 0.87$; Fig. 4).

At Smolikas, 329 newt stomachs were sampled from 80 female metamorphs, 86 female paedomorphs, 80 male metamorphs, and 83 male paedomorphs. They resulted in the identification of 17131 prey items. Six main prey categories were eaten by the newts: Crustacea (Daphniidae, Chydoridae, Calanoida, Cyclopoida, Ostracoda), pelagic Diptera (*Chaoborus* sp.), aquatic insect larvae (Chironomidae, Hemipteroidea, Ephemeroptera, and Dytiscidae), Bivalvia, Alpine newt eggs, and terrestrial invertebrates (Diptera, Coleoptera, Hemipteroidea, Hymenoptera, Arachnida). Diet composition differed between morphs in males (MANOVA, $F_{6,156} = 11.436$, $P < 0.001$) and females (MANOVA, $F_{6,159} = 9.451$, $P < 0.001$). Paedomorphic males and females preyed significantly more on aquatic insect larvae (Tukey's test, $P < 0.001$), and Bivalvia (U$P < 0.01$) than their metamorphic counterparts (Fig. 5). Paedomorphic males ingested more Crustacea ($P = 0.05$) and *Chaoborus* ($P < 0.001$) than metamorphic males, but this was not the case in females (Crustacea: $P = 0.13$, *Chaoborus*: $P = 0.23$; Fig. 5). Metamorphic females ingested significantly more newt eggs ($P < 0.001$) and more terrestrial invertebrates than paedomorphic females ($P < 0.05$; Fig. 5). Metamorphic males also ingested more eggs than paedomorphic males, but no difference was found for the terrestrial invertebrates ($P = 0.55$; Fig. 5).

3.4. Prey – predator movements

Newts co-migrated with their main pelagic prey, *Daphnia* sp. and *Chaoborus* sp., up to the water surface at dusk at Smolikas (Fig. 6). Thousands of newts were then seen breathing at the water surface. Planktonic organisms descended between midnight and dawn to the deepest layers of the water column. From 7 a.m. to 7 p.m. they concentrated near the bottom. During the night and the morning a higher proportion of newts was caught in the upper part of the water column. In the afternoon newts were caught in similar proportions throughout the water column. Floating newts caught prey at the surface only during daytime.

4. Discussion

Resource use differed between heterochronic morphs in the two studied Greek lakes, Tymphi and Smolikas. In general, paedomorphs focused mainly on pelagic crustaceans, whereas metamorphs foraged more on terrestrial invertebrates. Habitat use also differed, but not consistently across the two sites; however, metamorphs were more abundant at the water surface in both lakes.

Alpine newts foraged on all available prey items present in their environment, from small aquatic crustaceans to large aquatic insects and terrestrial invertebrates. The terrestrial invertebrates were caught by free-swimming newts at the water surface, a behavioural pattern frequently observed in oligotrophic lakes Chacornac and Joly, 1985 and Joly and Giacoma, 1992. Water mites (Hydracarina) were only found in the diet from newts caught in Tymphi, whereas pelagic Diptera larvae (*Chaoborus* sp.), Bivalvia, and newt eggs were only present in the diet in Smolikas. Such predation on newt eggs is quite common in the Alpine newt Sattmann, 1989 and Joly and Giacoma, 1992.

The two morphs differed in their prey spectrum in both the lakes, with paedomorphs eating predominantly pelagic invertebrates and metamorphs feeding more on prey at the water surface. Morphological heterochrony thus gives a structural and functional basis for variation in feeding behaviour. Similar to some fish species Hindar and Jonsson, 1982, Riget et al., 1986, Amundsen, 1988 and Malmquist et al., 1992 polymorphism in heterochronic newts is associated with food partitioning. This probably decreases competition for food and broadens the overall prey spectrum used by both morphs. This food partitioning may partly reflect the habitat use of newts in the same way that pelagic morphs of fishes forage on zooplankton and benthic morphs on zoobenthos Hindar and Jonsson, 1982, Riget et al., 1986, Amundsen, 1988 and Malmquist et al., 1992. Indeed, metamorphs were by far more abundant at the water surface, and, in Tymphi, more paedomorphs were found in the water column. However, as the same number of newts of the two morphs was selected for diet analysis in the different micro-habitats, the observed difference must be due to differences in prey selection. Such food partitioning was also found in La Cabane, a French alpine lake (Denoël and Joly, 2001). The two morphs also segregate in the use of other diet resources. In Smolikas, paedomorphs ate more insect larvae and newt eggs and less molluscs than metamorphs. In Tymphi, paedomorphic females ingested more water mites than metamorphic females.

As in La Cabane (Denoël and Joly, 2001), metamor-

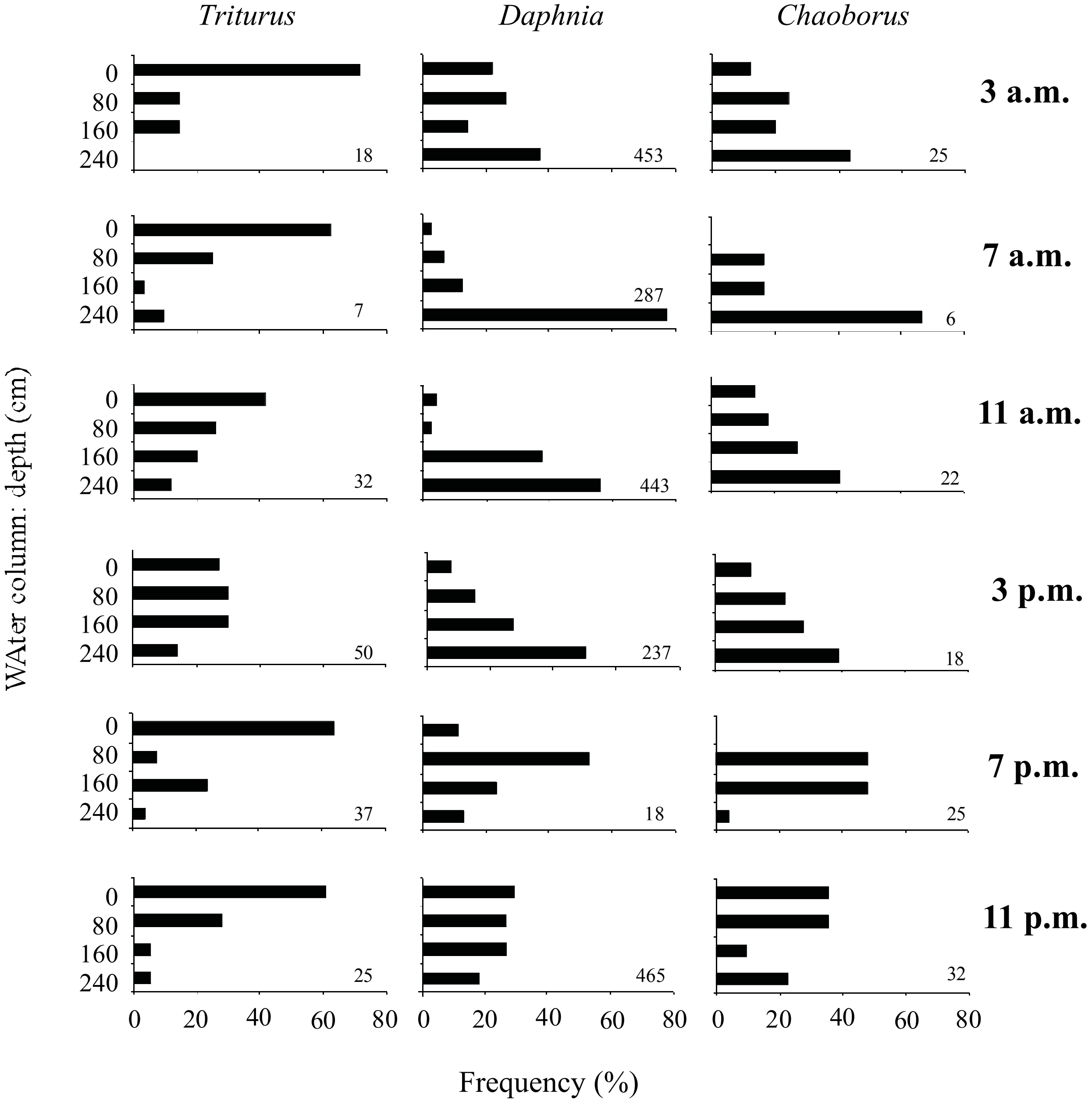


Figure 6. Proportion of newts, *Daphnia* sp., and *Chaoborus* sp. larvae at different sampling times and depths in the water column in Smolikas.

phs were more frequently found at the water surface in both Greek lakes. Additionally, a higher proportion of paedomorphs were caught in the open water in Tymphi. However, we did not detect strong differences in the use of the other micro-habitats, which is in accordance with observations of Breuil and Parent (1987). This is contrary to the situation observed in La Cabane (Denoël and Joly, 2001). In this lake, metamorphs were limited to the shallow bottom along the shore and the water surface, while paedomorphs moved in all micro-habitats including the deepest parts (7 m depth). In Tymphi and Smolikas, metamorphs did move into relatively deep micro-habitats. Such diving capabilities of metamorphs were also recorded in an Austrian alpine lake, where metamorphs were found at 9 m depth (Schabetsberger and Jersabek, 1995).

These traits confirm that paedomorphosis leads to habitat partitioning, but that the environmental conditions in a particular breeding site play an important role in determining the distribution of the two morphs. Tymphi and Smolikas are shallower than La Cabane (Denoël and Joly, 2001), which may have prevented such strong habitat partitioning as observed in La Cabane. The Greek lakes were also much warmer. While July water temperature at 7 m depth was 7 °C in the French Lake, it was 15 °C at 3.7 m depth in Smolikas (Denoël, 2001). Nothing is known about thermal preferences of the newts, except that low temperatures and darkness favour the paedomorphic process in the Alpine newt (Svob, 1965). The shallow areas of La Cabane contain numerous rocks under which newts can find shelter during daytime. On the other hand, there is comparatively little structure in the Greek lakes (particularly in Smolikas), where rocks are rare and mud covers most of the bottom. At Smolikas, the shoreline is covered by overhanging grass, but these shelters are limited and can only be occupied by a small part of the very large population. Metamorphs may have to move deeper along the slope area to obtain enough food and space. Population sizes in the Greek lakes (26,111 in Smolikas; 5491 in Tymphi) are much higher than in the French study site (1014); the volume of the French lake being higher than that of Smolikas or Tymphi (Denoël and Joly, 2000). Although less pronounced than in La Cabane, resource partitioning in the Greek lakes is still obvious and clearer than in more homogeneous habitats such as ponds Fasola and Canova, 1992, Fasola, 1993 and Denoël and Joly, 2000.

The proportion of paedomorphs in a natural population can vary or remain stable between years Denoël et al., 2001b and Denoël and Joly, 2001. When we compare our 1999 results with the censuses carried out by Breuil and Parent (1987) more than 10 years before our study, the relative proportions of the two morphs have not changed in Smolikas (74%) and has only slightly decreased in Tymphi (from 48% to 34%). The small difference at Tymphi might be due to differences in sampling techniques. However, laboratory experiments proved that crowding favours metamorphosis in *Ambystoma talpoideum* salamander larvae (Semlitsch, 1987) and *Notophthalmus viridescens* newt larvae (Harris, 1987), although this factor did not seem to be important in adult Alpine newts (Denoël, 2001). Long-term studies are needed to determine changes in populations where newt densities are high.

Alpine newts and their major pelagic prey (*Daphnia* and *Chaoborus*) ascended into shallower water at dusk. Such an increase in newt abundance close to the water surface in the evening was also reported by Breuil and Thuot (1983) and Breuil and Parent (1987). Most likely, newts ascended into shallower water to take advantage of the increased prey availability. Changes of micro-habitat in relation to prey densities have been shown in an Austrian lake inhabited by metamorphic Alpine newts (Schabetsberger and Jersabek, 1995). Predation or cannibalism are factors affecting micro-habitat use and vertical migration in tailed amphibians Toft, 1985, Stangel and Semlitsch, 1987 and Sih et al., 1992. Since Smolikas and Tymphi are devoid of fishes and other vertebrate predators, and since newts do not prey on adult conspecifics, their spatio-temporal distribution is not a strategy to avoid the risk of predation.

In conclusion, this study shows a correlation between morphological diversity and behavioural specialization, confirming previous expectations (Denoël and Joly, 2001). The two heterochronic morphs of Alpine newts differ in their use of space and food in both Greek lakes. However, our results also demonstrate the importance of habitat heterogeneity in determining resource use by alternative phenotypes.

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