

Trophic habits and aquatic microhabitat use in gilled immature, paedomorphic and metamorphic Alpine newts (*Triturus alpestris apuanus*) in a pond in central Italy

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ABSTRACT. Current evolutionary models suggest that the presence of heterogeneous habitats favours the evolution of polymorphisms. In such cases, alternative phenotypes can coexist because they use different resources. Facultative paedomorphosis is a heterochronic polymorphism in which a morph – the paedomorph – retains larval traits during the adult stage while the other morph – the metamorph – is fully metamorphosed. The aim of this study was to determine the microhabitat use and the diet of Alpine newt paedomorphs, metamorphs and immatures (*Triturus alpestris apuanus*) coexisting in a small pond in Tuscany, central Italy, i.e. in a habitat where dimorphism is not expected. Although the two adult morphs do not use exactly the same resources, resource partitioning was weaker than in deep Alpine lakes. Nevertheless, the diet of immature gilled newts (larvae) differed from that of adults (metamorphs and paedomorphs). While the larvae eat a large number of planktonic organisms, the adults focus on insect larvae and newt eggs. The differences in resource use favour the coexistence of aquatic juveniles and adults. In the studied pond, facultative paedomorphosis was previously shown to be favoured by a precocious maturity of the paedomorphs. This study shows that the coexistence of paedomorphs and metamorphs may also be supported by some dietary and spatial segregation, although any advantages gained by this pattern are rather limited in the adult stage.

KEY WORDS : facultative paedomorphosis, resource partitioning, habitat, diet, size-selective predation, vacant niches, density regulation, newt.

INTRODUCTION

Newts live under water during the breeding period and adopt a terrestrial life during the rest of the year (GRIFFITHS, 1996). Food and microhabitat use in the aquatic phase have been largely studied in the species of genus *Triturus* (see e.g. GRIFFITHS & MYLOTTE, 1987; JOLY & GIACOMA, 1992). Newts often play the role of top predators (SCHABETSBERGER & JERSABEK, 1995). Their diet is wide, newts eating prey such as small crustaceans, molluscs, aquatic insect larvae, and aquatic insects (JOLY, 1987a). Furthermore, they can also forage on amphibian eggs laid in the aquatic habitat (Joly, 1987a; SATTMANN, 1989; JOLY & GIACOMA, 1992) and on terrestrial invertebrates that fall to the water surface (CHACORNAC & JOLY, 1985; SATTMANN, 1989; JOLY & GIACOMA, 1992; SCHABETSBERGER & JERSABEK, 1995). They can occupy all aquatic micro-habitats, i.e. the shoreline, the water column, the water surface and the bottom of lakes up to nine meters deep (SCHABETSBERGER, 1993; DENOËL & JOLY 2001a).

Although they can be largely opportunistic, newts can also select microhabitats and prey according to specific taxa or sizes (AVERY, 1968; JOLY & GIACOMA, 1992; BRAZ & JOLY, 1994). In ponds where up to five newt species can be found (ARNTZEN & DE WIJER, 1989), such habitat and prey selection might reduce species competi-

tion and then favour their coexistence (SCHOENER, 1974; TOKESHI, 1999). Resource partitioning has been observed in several newt communities composed of two (DOLMEN & KOKSVIK, 1983; GRIFFITHS & MYLOTTE, 1987; DOLMEN, 1988) and three species (JOLY & GIACOMA, 1992; FASOLA, 1993; BRAZ & JOLY, 1994). However, large niche overlaps were also found in other newt communities (BRAÑA et al., 1986; GRIFFITHS, 1986, 1987; JEHL et al., 2000).

The life cycle of newts is complex and composed of a pre-metamorphic larval stage and a post-metamorphic juvenile and adult stage (GRIFFITHS, 1996). However, in some populations, individuals forgo metamorphosis and reproduce in the larval stage (facultative paedomorphosis) (SEMLITSCH & WILBUR, 1989; BREUIL, 1992; WHITEMAN, 1994). In Europe such a process is known in *Triturus* newts, including Italian populations of *T. alpestris* (DUBOIS & BREUIL, 1983; ANDREONE & DORE, 1991; ANDREONE et al., 1993; DENOËL et al. 2001b). Paedomorphosis has been shown to be favoured in permanent aquatic habitats at low densities (HARRIS, 1987; SEMLITSCH, 1987) and when prey are abundant (DENOËL & PONCIN, 2001). Early maturation of paedomorphs (RYAN & SEMLITSCH, 1998; DENOËL & JOLY, 2000), resource partitioning between morphs (WHITEMAN et al., 1996; DENOËL et al., 1999; DENOËL & JOLY, 2001a), high energy intake (DENOËL et al., 2002), different breeding

frequencies (WHITEMAN, 1997) and sexual activities in the two morphs (DENOËL et al., 2001a) also favour the maintenance of facultative paedomorphosis in natural populations.

Resource polymorphisms are expected to be promoted in heterogeneous habitats devoid of competitors (SKULASON & SMITH, 1995; SMITH & SKULASON, 1996). This hypothesis is supported by empirical data in fishes (MALMQUIST, 1992; MALMQUIST et al., 1992; ROBINSON et al., 1993), and also in newts (DENOËL et al., 1999, 2001b; DENOËL & JOLY, 2001a). Intramorphic differences in diet were also shown to favour coexistence of larval and paedomorphic newts in one of these lakes (DENOËL & JOLY, 2001b). However, in less complex habitats, space and feeding habits of paedomorphs and metamorphs have been poorly studied (e.g., FASOLA & CANOVA, 1992) and no study has examined resource use in such sites occupied by only one species.

The aim of the present study was to determine the feeding and space habits of paedomorphic, metamorphic and immature gilled Alpine newts (*Triturus alpestris apuanus* [Bonaparte, 1839]) (Amphibia, Caudata, Salamandridae) coexisting in a habitat devoid of diversified components: a small pond. The comparisons of these traits in alternative heterochronic morphs will help us to understand the maintenance of facultative metamorphosis in such natural populations. Particularly, we expect large overlaps in resource use between adult morphs due to the small depth of the studied pond, but some partitioning between larval and adult stages because of size differences.

MATERIAL AND METHODS

The study site is located in the Apennines close to Parana (municipality of Mulazzo, Province of Massa Carrara, Tuscany, Italy; 44°17'N/9°51'E), at an elevation of 600 m a.s.l. It is a small, shallow pond (maximum depth: 0.7 m, surface: 200 m²; Fig. 1). Water level may decrease in summer, or, on some occasions, even dry up. The pond comprised two main microhabitats: an open area devoid of vegetation and an area covered with aquatic plants (*Glyceria*, *Typha*). The water surface freezes in winter, including at the beginning of the breeding season when there are still heavy snowfalls (March). The pond is surrounded by pastures and in the proximity of deciduous forests (around one hundred meters). It is devoid of fish and no water snakes were observed during the study. The newt community is only composed of Alpine newts *Triturus alpestris apuanus*, although we found a single individual of *Triturus carnifex carnifex* (DENOËL et al., 2001b).

Five types of Alpine newt could be distinguished in the population: (1) (2) the male and female metamorphs, (3) (4) the male and female paedomorphs, and (5) the gilled larvae, also called gilled juveniles (overwintering individuals in the present analysis). Both paedomorphs and metamorphs were indeed sexually mature, as shown by behavioural analyses (BOVERO et al., 1997; pers. obs.). Adulthood was here defined by the presence of a well developed cloaca (vs. a slit in juveniles). No metamorphosed juveniles were observed.



Fig. 1. – The study site (Parana, Tuscany, Italy; March 1997).

Newts were sampled with a landing net from an inflatable dinghy. Sampling effort was distributed according to a three-way design: (i) month, (ii) time of day, and (iii) microhabitat. Two microhabitats were sampled during each sampling session: the open area and the area covered by vegetation. Sampling lasted 20 minutes in each microhabitat and was carried out four times a day: at dawn (0600 hr), at mid-day (1200 hr), at the end of the day (1800 hr) and at midnight (0000 hr). Five sampling sessions were carried out in March 1997 (the fifth session at 1200 hr) and eight in April 1997 (two at each sampling time). These months correspond to the breeding period of the newts. At that time, both paedomorphs and metamorphs coexisted under water. Metamorphs are terrestrial outside the reproductive period. Captured newts were then stocked in four large containers filled with water from the pond. Immediately after the capture, a number of these animals (about eight individuals of each morph) were randomly drawn and anaesthetized in a solution of phenoxyethanol (0.5%). Stomach contents were then collected using a non-invasive stomach-flushing procedure (JOLY, 1987b) and stocked in separate vials containing formaldehyde (4%). Prey were subsequently identified (at the species, genus, family or order level depending on taxa) and measured (total length) on squared paper under a stereoscopic microscope. Newts were measured (snout-vent length, SVL to the nearest mm) with a metal rule.

As data did not fit normal distributions, we used the Mann-Whitney *U*-test for all statistical comparisons of independent samples. Our samples being large and containing ties, we computed the normal approximation of the *U*-test. We also used Spearman rank correlation with associated *t*-test to determine the significance of relationships between variables. A chi-square test was performed to test for equal distribution of newts in the two microhabitats (SIEGEL & CASTELLAN, 1988; STATSOFT FRANCE, 2000).

Prey niche overlap between morphs was calculated using SCHOENER's (1970) index, which has already been used in newt ecology studies (GRIFFITHS & MYLOTTE, 1987; FASOLA, 1993):

$$C = 1 - 0.5 \left(\sum_i |p_{xi} - p_{yi}| \right)$$

where p_{xi} is the proportional utilization of prey type i by morph x , and p_{yi} the proportional utilization of prey type i by morph y . The index ranges from 0 (no prey in common) to 1 (all prey in common).

RESULTS

The four different forms of adult newt ($N = 358$) inhabited both the open and vegetation areas. Nevertheless, they significantly differed in the use of these microhabitats ($\chi^2 = 18.3$, 3 d.f., $p < 0.001$; Fig. 2). The pedomorphs were proportionally more abundant in the vegetation area ($\chi^2 = 12.82$, 1 d.f., $p < 0.001$; Fig. 2).

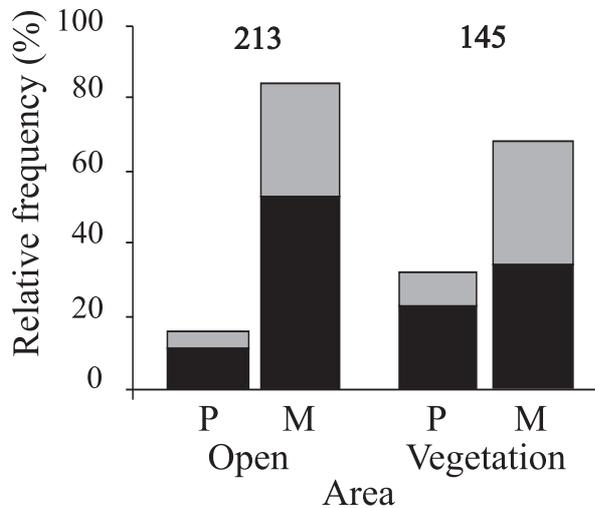


Fig. 2. – Spatial use of the two main microhabitats (open and vegetation areas) in the Parana pond in April 1997. P: pedomorph, M: metamorph; black bars: females, open bars: males.

The distribution of newts significantly differed at midday ($\chi^2 = 10.59$, 3 d.f., $p < 0.05$; Fig. 3) and at the end of the day ($\chi^2 = 11.51$, 3 d.f., $p < 0.01$; Fig. 3), but not at midnight ($\chi^2 = 3.68$, 3 d.f., NS; Fig. 3) or at dawn ($\chi^2 = 2.09$, 3 d.f., NS; Fig. 3). At midday and in the evening, pedomorphs were proportionally more abundant in the vegetation (respectively, $\chi^2 = 7.39$, 1 d.f., $p < 0.01$ and $\chi^2 = 10.14$, 1 d.f., $p < 0.01$).

A total of 7827 prey were obtained from the 296 newts (254 adults and 42 juveniles). The prey consisted mainly of crustaceans (Chydoridae, Cyclopoida, Ostracoda), insect larvae (chironomid and ceratopogonid Diptera, Plecoptera, Zygoptera, dytiscid and helodid Coleoptera), Alpine newt eggs, and sloughs of common toad *Bufo bufo* and newt *Triturus alpestris* (Fig. 4).

From a qualitative point of view, the two adult morphs foraged on the same kinds of prey (Table 1 and 2). Food niche overlap was also quite large: 0.75 between pedomorphic and metamorphic females and 0.74 between pedomorphic and metamorphic males. From a quantitative point of view, there were almost no significant differences between the two adult morphs (U -test, Table 1 and 2). Pedomorphic and metamorphic females significantly differed in prey use for chironomid, helodid and Zygoptera larvae, but not for the other prey (U -test, Table 1).

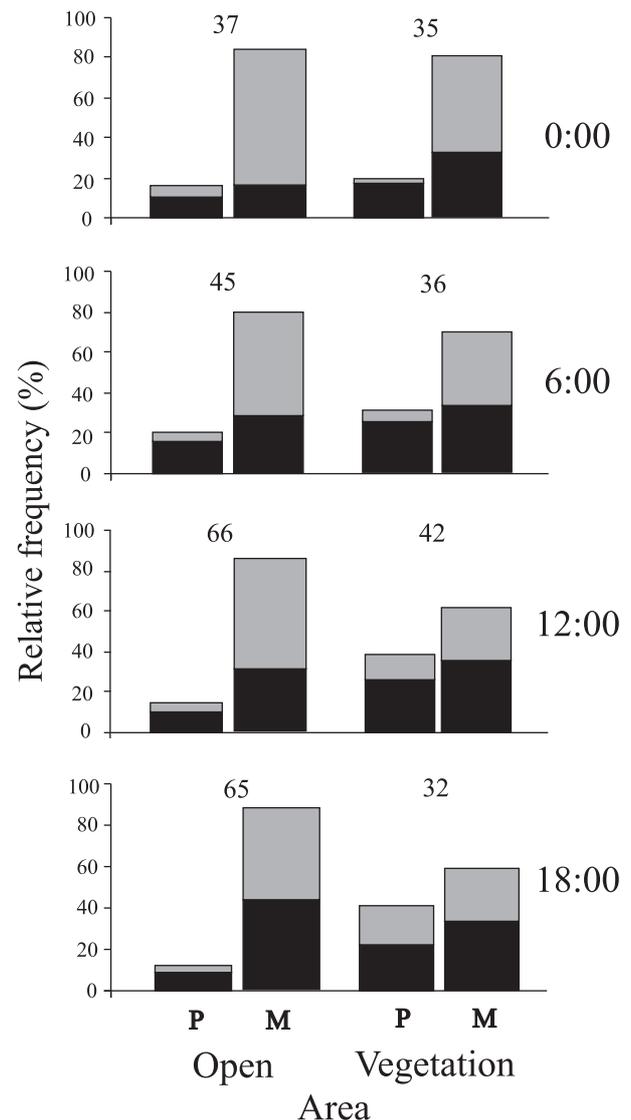


Fig. 3. – Temporal use of the two main microhabitats (open and vegetation areas) in the Parana pond in April 1997: at midnight, dawn, mid-day and in the evening. P: pedomorph, M: metamorph; black bars: females, open bars: males.

The large mean number of *Chydorus* in pedomorphic females was due to only one individual that ate 259 specimens of this taxon. Pedomorphic and metamorphic males significantly differed in prey use of Chydoridae, Cyclopoida and amphibian sloughs, but not for the other prey (U -test, Table 2). In all significant cases, the scores were higher in the pedomorphs than in the metamorphs.

Significant differences were also observed between the two different sampling dates. In females, they concern only chironomid larvae. Other significant differences were found only in March for chironomid pupae and Zygoptera larvae, and in April for helodid and dytiscid larvae (Table 1). In males, no significant differences were found over the two months. In March, the two morphs differed in terms of amphibian sloughs and in April for chydorids, Cyclopoida and helodid larvae (Table 2). In females of the two morphs, food niche overlap was 0.66 in March and 0.68 in April. In males, it was 0.67 in March and 0.61 in April.

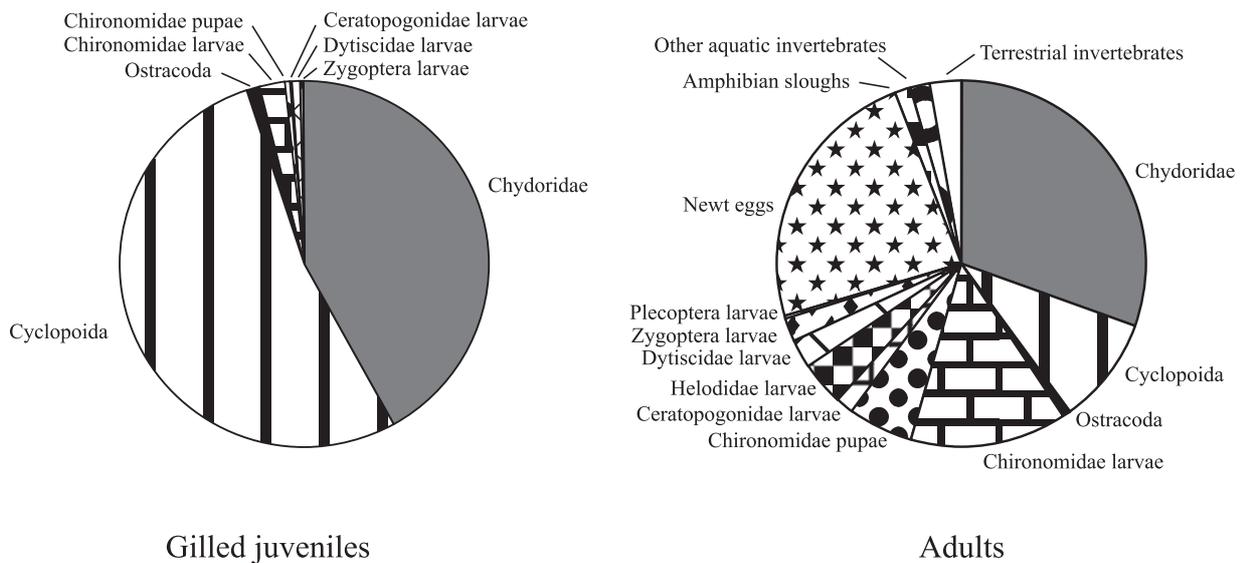


Fig. 4. – Relative composition of the gut contents of gilled juveniles ($N = 42$) and adults (paedomorphs and metamorphs; $N = 254$) in the Parana pond (March/April 1997). Prey accounting for less than 0.1 percent of the diet are not represented (i.e. Helodidae larvae, other aquatic and terrestrial invertebrates in branchiate juveniles). The large proportion of *Chydorus* in adults is due to only one individual.

Paedomorphic females consumed significantly more chironomid larvae ($p < 0.05$) and dytiscid larvae ($p < 0.01$) in the open area and more helodid larvae in the vegetation area ($p < 0.05$) than metamorphic females did (U -test). Paedomorphic males consumed significantly more Cyclopoida and helodid larvae in the open area ($p < 0.01$) and more *Chydorus* ($p < 0.01$) in the vegetation area than metamorphic males did (U -test).

There was no significant difference in diet between the two morphs, in males and females, in the midnight sample (U -test). Significant differences were found in the three other samples, except for males at dawn. Paedomorphic females ate significantly more chironomid larvae at dawn (U -test; $p < 0.01$) and midday; more helodid larvae at dawn and in the evening; and more dytiscid larvae at dawn and midday than the metamorphic females (U -test; $p < 0.05$). Stomachs of paedomorphic males contained more *Chydorus* ($p < 0.05$) and chironomid larvae ($p < 0.01$) at midday, and more amphibian sloughs in the evening than those of metamorphic males (U -test; $p < 0.05$).

Gilled juveniles ingested significantly more *Chydorus*, Cyclopoida, Ostracoda, and chironomid and dytiscid larvae than the adults (paedomorphs and metamorphs taken together), but they consumed fewer newt eggs (U -test, $p < 0.001$ for each of the six comparisons; Fig. 4). Food niche overlap was only 0.25 between adults and gilled juveniles.

There was a significant correlation between the size of the prey and the size of the newts (all individuals considered: $r_S = 0.32$, $t_{276} = 5.620$, $p < 0.001$). Mean size of the prey caught by paedomorphic and metamorphic males (5.9 mm and 7.5 mm respectively, U -test, $p = 0.05$) and by paedomorphic and metamorphic females did not differ significantly (6.9 mm and 8.6 mm respectively, U -test, $p = 0.5$), but differed between branchiate juveniles and adults (mean = 2.7 mm and 7.3 mm respectively, U -test, $p < 0.001$).

DISCUSSION

From our study it is evident that some differences were found in both spatial and food use between paedomorphic and metamorphic Alpine newts. Paedomorphs preferred the microhabitats with aquatic vegetation, while metamorphs preferred the open area devoid of vegetation. Some prey taxa were used differentially by the two morphs but not consistently across the sexes (chironomid, helodid, dytiscid and Zygoptera larvae in females and chydorids, Cyclopoida and amphibian sloughs in males). However, resource partitioning is difficult to interpret, since it is rather limited and does not appear in all subsamples. The overlap for food use between the adult morphs ranged between 0.61 and 0.75 (SCHOENER's Index, 1970). The two morphs were largely present in the two microhabitats and qualitatively used the same prey (i.e. mainly insect larvae and newt eggs, plankton being under-exploited). In fact, the difference in prey use was due to a larger capture rate by paedomorphs. Indeed, all significant comparisons between the two morphs revealed a higher mean prey number per stomach in paedomorphs than in metamorphs.

These results differ from those obtained in a deep Alpine lake (La Cabane lake, France). In such a diversified aquatic habitat containing a vertical component, paedomorphs foraged in all the micro-habitats, but metamorphs were limited to peripheral areas. The diet of paedomorphs was mainly composed of planktonic organisms (e.g., daphnids, Cyclopoida, chirocephalids). Metamorphs relied for a large part on terrestrial invertebrates that fell to the water surface of the lake (DENOËL et al., 1999; DENOËL & JOLY, 2001a). Although less pronounced, a similar degree of diet and habitat segregation was also found in two other Alpine lakes in Greece (DENOËL, 2001). As in our study, FASOLA & CANOVA (1992) found a large overlap in food resources in the adult morphs occupying small ponds inhabited by three species

TABLE 1

Stomach contents of female paedomorphs ($N = 35$ in March, $N=40$ in April) and metamorphs ($N = 29$ in March, $N = 39$ in April) in a small Italian pond (Z -adjusted Mann-Whitney U -test)

Prey taxa	Month	Paedomorphs Mean (min – max)	Metamorphs Mean (min – max)	Z -adj.	P
Chydoridae	March	0	0.1 (0-2)	-1.100	0.27
	April	7.2 (0-259 ^a)	0.2 (0-4)	1.534	0.12
	Total	3.8 (0-259 ^a)	0.1 (0-4)	0.980	0.32
Cyclopoida	March	0.4 (0-6)	0.5 (0-5)	-0.939	0.34
	April	1.2 (0-16)	0.3 (0-4)	1.643	0.10
	Total	0.8 (0-16)	0.4 (0-5)	0.652	0.51
Ostracoda	March	0.1 (0-1)	0.1 (0-1)	0.25	0.81
	April	0.03 (0-1)	0.1 (0-1)	-0.607	0.54
	Total	0.1 (0-1)	0.1 (0-1)	-0.142	0.89
Chironomidae larvae	March	1.4 (0-6)	0.4 (0-3)	2.860	<0.01
	April	1.2 (0-7)	0.5 (0-5)	2.004	<0.05
	Total	1.4 (0-7)	0.5 (0-5)	3.437	<0.001
Chironomidae pupae	March	1.4 (0-11)	0.4 (0-5)	2.040	<0.05
	April	0.4 (0-3)	0.6 (0-4)	-1.031	0.30
	Total	0.8 (0-11)	0.5 (0-5)	0.767	0.44
Ceratopogonidae larvae	March	0.1 (0-2)	0.1 (0-2)	-0.200	0.84
	April	0.1 (0-1)	0.1 (0-1)	0.430	0.67
	Total	0.1 (0-2)	0.1 (0-1)	0.166	0.87
Helodidae larvae	March	0.9 (0-15)	0.4 (0-6)	1.345	0.18
	April	0.8 (0-14)	0	3.313	<0.001
	Total	0.8 (0-15)	0.2 (0-6)	3.265	<0.01
Dytiscidae larvae	March	0.2 (0-2)	0.1 (0-1)	0.910	0.13
	April	0.3 (0-3)	0.03 (0-1)	2.873	<0.01
	Total	0.3 (0-3)	0.04 (0-1)	3.158	<0.01
Zygoptera larvae	March	0.3 (0-4)	0	2.530	<0.05
	April	0.3 (0-2)	0.1 (0-1)	1.487	0.13
	Total	0.3 (0-4)	0.1 (0-1)	2.675	<0.01
Plecoptera larvae	March	0.2 (0-2)	0.2 (0-2)	0.670	0.50
	April	0	0.1 (0-2)	-1.012	0.31
	Total	0.1 (0-2)	0.1 (0-2)	0.430	0.67
Alpine newt eggs	March	1.0 (0-9)	1.3 (0-15)	0.027	0.98
	April	2.2 (0-13)	2.4 (0-17)	0.555	0.58
	Total	1.6 (0-13)	1.9 (0-17)	0.388	0.70
Amphibian sloughs	March	0.3 (0-1)	0.3 (0-1)	-0.758	0.45
	April	0.1 (0-1)	0.1 (0-1)	-0.032	0.97
	Total	0.2 (0-1)	0.2 (0-1)	-0.488	0.625
Other aquatic invertebrates	March	0.4 (0-3)	0.3 (0-5)	0.923	0.36
	April	0.2 (0-2)	0.2 (0-2)	0.258	0.80
	Total	0.2 (0-3)	0.2 (0-5)	0.904	0.37
Terrestrial invertebrates	March	0.1 (0-2)	0.2 (0-1)	-0.604	0.55
	April	0.3 (0-2)	0.2 (0-2)	0.665	0.51
	Total	0.2 (0-2)	0.2 (0-2)	0.145	0.89

TABLE 2

Stomach contents of male paedomorphs ($N = 17$ in March, $N=27$ in April) and metamorphs ($N = 30$ in March, $N = 37$ in April) in a small Italian pond (Z -adjusted Mann-Whitney U -test)

Prey taxa	Month	Paedomorphs Mean (min – max)	Metamorphs Mean (min – max)	Z -adj.	P
Chydoridae	March	0	0	-	-
	April	0.6 (0-4)	0.1 (0-1)	2.692	<0.01
	Total	0.4 (0-4)	0.03 (0-1)	2.768	<0.01
Cyclopoida	March	1.4 (0-12)	0.4 (0-4)	0.135	0.89
	April	1.4 (0-13)	0.1 (0-2)	2.589	<0.01
	Total	1.4 (0-13)	0.3 (0-4)	1.969	<0.05
Ostracoda	March	0	0.1 (0-1)	-1.076	0.28
	April	0.1 (0-1)	0.03 (0-1)	1.362	0.17
	Total	0.1 (0-1)	0.05 (0-1)	0.531	0.59
Chironomidae larvae	March	1.1 (0-4)	0.9 (0-3)	0.366	0.71
	April	1.1 (0-5)	1.1 (0-6)	0.111	0.91
	Total	1.1 (0-5)	1.0 (0-6)	0.289	0.77
Chironomidae pupae	March	0.8 (0-4)	0.3 (0-2)	0.812	0.42
	April	0.2 (0-3)	0.4 (0-4)	-0.941	0.35
	Total	0.4 (0-4)	0.3 (0-4)	-0.211	0.83
Ceratopogonidae larvae	March	0.2 (0-2)	0.2 (0-2)	-0.393	0.69
	April	0.2 (0-3)	0.1 (0-1)	0.203	0.84
	Total	0.2 (0-3)	0.2 (0-2)	-0.114	0.91
Helodidae larvae	March	0.3 (0-2)	0.4 (0-5)	0.320	0.75
	April	0.3 (0-1)	0.03 (0-1)	2.753	<0.01
	Total	0.3 (0-2)	0.2 (0-5)	1.0909	0.06
Dytiscidae larvae	March	0.2 (0-1)	0.5 (0-3)	-1.428	0.15
	April	0.3 (0-2)	0.1 (0-1)	1.315	0.19
	Total	0.3 (0-2)	0.3 (0-3)	-0.206	0.84
Zygoptera larvae	March	0.1 (0-1)	0	1.328	0.18
	April	0.1 (0-1)	0.1 (0-1)	0.038	0.97
	Total	0.1 (0-1)	0.1 (0-1)	0.619	0.54
Plecoptera larvae	March	0	0.03 (0-1)	-0.753	0.45
	April	0.03 (0-1)	0	1.171	0.24
	Total	0.02 (0-1)	0.02 (0-1)	0.301	0.76
Alpine newt eggs	March	0.1 (0-1)	0.1 (0-1)	-0.503	0.61
	April	0.9 (0-4)	1.0 (0-16)	0.860	0.39
	Total	0.6 (0-4)	0.6 (0-16)	0.785	0.43
Amphibian sloughs	March	0.6 (0-2)	0.2 (0-1)	2.374	<0.05
	April	0.2 (0-1)	0.1 (0-1)	1.234	0.22
	Total	0.3 (0-2)	0.1 (0-1)	2.363	<0.05
Other aquatic invertebrates	March	0.1 (0-1)	0.4 (0-4)	-0.590	0.55
	April	0.2 (0-1)	0.03 (0-1)	1.769	0.08
	Total	0.1 (0-1)	0.2 (0-4)	0.638	0.52
Terrestrial invertebrates	March	0	0.1 (0-1)	-1.076	0.28
	April	0.2 (0-1)	0.1 (0-1)	0.147	0.83
	Total	0.1 (0-1)	0.1 (0-1)	-0.233	0.82

Chydoridae are Cladocera, Cyclopoida are Copepoda, Helodidae and Dytiscidae are Coleoptera, Chironomidae and Ceratopogonidae are Diptera. Amphibian sloughs are from *Triturus alpestris* and *Bufo bufo*. Z adj. = Z adjusted.

^a Large value due to only one individual.

of newts (*Triturus alpestris apuanus*, *Triturus vulgaris meridionalis* and *Triturus c. carnifex*). These characteristics support the hypothesis that the presence of varied underexploited microhabitats favours resource partitioning (MALMQUIST et al., 1992; ROBINSON et al., 1993; SKULASON & SMITH, 1995), but show that the presence of such heterogeneity is not an obligate prerequisite for the maintenance of polymorphisms. Alternative explanations have thus to be found, particularly in the life-history of the newts coping with habitat uncertainty (KALEZIC & DZUKIC, 1985; DENOËL & JOLY, 2000; DENOËL et al., 2002).

Apennine ponds are small aquatic habitats devoid of a vertical component, in contrast to Alpine lakes, which are often very deep (e.g. 7 m depth : DENOËL & JOLY, 2001a). Consequently, in a rather homogeneous environment, alternative phenotypes might profit less from their morpho-physiological status (e.g. trophic apparatus, gills, and body shape), even in the absence of newt competitors as is the case in the studied pond (DENOËL et al., 2001b). In the absence of deep waters, paedomorphs have also no possibility to avoid competition with metamorphs in shallow waters. Differences in habitat and food use between

alternative morphs within a species have been shown in animal groups other than the amphibians. For instance, in the bluegill (*Lepomis macrochirus*), individuals differ in the size of their pectoral fins. This specialization gives them specific foraging advantages: in open water for the individuals with short fins and in vegetated areas for the individuals with long fins. The two morphs are also observed in the micro-habitat where they are expected (EHLINGER, 1990). However, in heterochronic newts, no morphological trait supports the higher abundance of paedomorphs in the vegetation area than in the open area. Indeed, paedomorphs would be particularly expected in open water. Such habitat preference might be connected to some foraging tactics because prey distribution differs between the two habitat components (M. DENOËL, pers. obs.), but laboratory experiments are needed to test this hypothesis.

Paedomorphs and metamorphs possess a different feeding mechanism. In both morphs, prey items are sucked in with water, but metamorphs have to expel water out of the mouth after suction because their gill slits are closed (JOLY, 1981; LAUDER & SHAFFER, 1993). These morphological differences lead to differences in efficiency of catching prey: paedomorphs are better predators on crustaceans whereas metamorphs are more efficient at catching terrestrial invertebrates (DENOËL, 2001). Despite these characteristics, paedomorphs do not eat many more plankton (except in April in males) and less terrestrial invertebrates than metamorphs in the studied pond. In fact, although planktonic organisms were relatively abundant (around twenty individuals per litre) in the eutrophic pond, adults caught only a few individuals each day. This means that far fewer plankton were eaten than in Alpine lakes where plankton was an important element of the diet (around sixty planktonic individuals per paedomorph stomach: DENOËL et al., 1999; DENOËL & JOLY, 2001a). This lack of utilisation of small prey might originate from the abundance of other prey in the diet of newts (e.g., chironomid larvae and newt eggs) (JOLY, 1987a). Higher ingestion rates of chironomid larvae in paedomorphs than in metamorphs were also shown in experimental trials (DENOËL, 2001). In the studied pond, terrestrial invertebrates were very rare, suggesting that metamorphs are not particularly specialized on this diet. On the contrary, in oligotrophic Alpine lakes, terrestrial invertebrates are abundant during the aquatic active period of the newts, and comprise a large part of the diet of the newts (CHACORNAC & JOLY, 1985; SATTMANN, 1989; JOLY & GIACOMA, 1992; SCHABETSBERGER & JERSABEK, 1995).

The diet of newts was not identical in March and April. These differences were mainly due to variation in prey abundance between these two months. For instance, the small number of newt eggs consumed in March was due to the oviposition period of the newts, which was more intense in April than in March. More amphibian sloughs were foraged in March as a consequence of the adaptation of the newts to their new environment (GRIFFITHS, 1996) and to the presence of common toads *Bufo bufo* only in March. Large densities of prey might also increase resource overlap (HINDAR & JONSSON, 1982; GRIFFITHS, 1986; SMITH, 1990), but similar food niche overlaps between morphs were found in March and April.

Eggs of newts are usually laid in the aquatic vegetation (MIAUD, 1995), increasing their survival against invertebrate and vertebrate predators (MIAUD, 1993, 1994). However, Alpine newts foraged particularly on this kind of prey. Considering fecundity of Alpine newts (a few tens to hundreds of eggs: KALEZIC et al., 1996) and the large number of eggs eaten (more than one egg per newt per day in this study), this predation affects general productivity and potentially limits the population size. In the studied site, newt density was very high: more than 2000 newts for a 100 m³ pond. This predation mechanism might then be regulated by population density. It is also mainly exhibited by females, as previously outlined by other authors (JOLY, 1987a; SATTMANN, 1989; JOLY & GIACOMA, 1992). Kin selection experiments suggests that some amphibian species avoid eating their own progeny (BLAUSTEIN & WALLS, 1995). However, no kin selection was found in the smooth newt (GABOR, 1996), and the situation remains unknown in the Alpine newt.

Variation in body size, and thus in the gape width, can favour resource partitioning (HUTCHINSON, 1959). Numerous examples have been found in newts and salamanders (LEFF & BACHMAN, 1986; KUZMIN, 1991; JOLY & GIACOMA, 1992), including in paedomorphic communities (FASOLA & CANOVA, 1992; DENOËL & JOLY, 2001b). Paedomorphs from the studied site are younger and smaller than the metamorphs (DENOËL & JOLY, 2000). However, the difference in size (12 % in females, 7 % in males) does not appear to be related to predation tactics because the two morphs foraged on similar-sized prey. On the contrary, gilled juveniles largely differ from adults in diet use. They eat many more cladocerans and copepods than the adults, but also a few more insect larvae. The smallest gilled juveniles (23–34 mm) ate only small prey (mean prey length of about 1 mm), but the largest gilled juveniles behave more similarly to adults in eating different-sized prey (mean prey length of about 1 to 13 mm). Differences are related more to the size of individuals than to the acquisition of maturity. Mean prey size of adults was about 1 to 20 mm. There is thus an obvious resource partitioning between the two gilled immature classes and between gilled immature and adult stages. The avoidance of planktonic organisms by adults favours gilled juveniles, which are gape-limited. The limited trophic similarities between the gilled juveniles and the paedomorphs therefore favours the maintenance of paedomorphs in the ponds as the two have to coexist all the year round, in contrast to the metamorphs that leave the pond after breeding (M. DENOËL, pers. obs.).

In the studied site, paedomorphs gain fitness benefits from their earlier age at maturity (DENOËL & JOLY, 2000), but interfere with metamorphs in using similar dietary items and habitat components (this study). Once they mature in larval morphology, they can still gain advantages from resource partitioning but this benefit seems limited. However, paedomorphs gain high body condition and energy intake, which make the paedomorphic pathway advantageous in this habitat (DENOËL et al., 2002) until the risk of the pond drying out and the high densities (12 individuals/m² in the studied pond) might make the site undesirable and then favour metamorphosis and dispersion of the paedomorphs (DENOËL & PONCIN, 2001; DENOËL, 2001).

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