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Diet of larval *Pleurodeles waltl* (Urodela: Salamandridae) throughout its distributional range

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ABSTRACT

Diet of larval *Pleurodeles waltl* (Urodela: Salamandridae) throughout its distributional range

Larval diet has important implications for assessing suitable reproduction habitats for amphibians. In this study we investigated the diet of larvae of the Iberian ribbed newt (*Pleurodeles waltl*), an urodele endemic of the western Mediterranean region. We examined the stomach contents of 150 larvae captured in 30 ponds in Spain, Portugal and Morocco. We found that the larvae predate primarily on microcrustaceans (Cladocera, Ostracoda and Copepoda) and larvae of aquatic insects (Chironomidae, Culicidae and Dytiscidae). However, *P. waltl* was found to have a broad dietary range, including terrestrial Arthropoda (Homoptera, Sminthuridae and Formicidae), Gastropoda (Physidae and Planorbidae) and amphibian larvae (Anura and Urodela). As expected, larger larvae had a more diverse diet, as they can capture larger prey.

Key words: insect larvae, microcrustaceans, Morocco, ribbed newt, trophic range

RESUMEN

Dieta larvaria de* Pleurodeles waltl *(Urodela: Salamandridae) a través de su rango de distribución

*La dieta larvaria tiene implicaciones importantes para evaluar la idoneidad de los hábitats de reproducción de los anfibios. En este estudio investigamos la dieta larvaria del gallipato ibérico (*Pleurodeles waltl*), un urodelo endémico del Mediterráneo occidental. En 150 larvas capturadas en 30 charcas temporales en España, Portugal y Marruecos los microcrustáceos (Cladocera, Ostracoda y Copepoda) y larvas de insectos acuáticos (Chironomidae, Culicidae y Dytiscidae) son los ítems numéricamente dominantes. Sin embargo* P. waltl *muestra un amplio rango trófico, incluyendo también algunos Arthropoda terrestres (Homoptera, Sminthuridae y Formicidae), Gastropoda (Physidae y Planorbidae) y larvas de anfibios (Anura y Urodela). Las larvas de mayor tamaño tienen una dieta más diversificada, que incluye presas más grandes.*

Palabras clave: *gallipato, larvas de insecto, Marruecos, microcrustáceos, rango trófico*

INTRODUCTION

Numerous species of amphibians occupy distinct ecological niches in both their adult and larval phases, and exploit very different trophic resources (Davic, 1991; Wells, 2010). Larvae of urodeles are aquatic and carnivorous, and have long development phases (usually exceeding 2–3 months; Petranka, 1998). During development larvae undergo several morphological changes, including a significant increase in body size (Galien & Durocher, 1957). Larval development is also associated with dietary changes, because larger body sizes enable larvae to feed on larger prey, including conspecifics (Kusano *et al.*, 1985; Whiteman *et al.*, 1996). Urodele larvae feed on several types of aquatic invertebrates and tadpoles, and so play a key role as apex predators in temporary lentic communities (Holomuzki & Collins, 1987; Durant & Hopkins, 2008).

The Iberian ribbed newt *Pleurodeles waltl* is an endemic urodele of the western Mediterranean region (Iberian Peninsula and Atlantic region of Morocco; Escoriza & Ben Hassine, 2015). This species breeds in temporary but relatively long-lasting ponds (approximately 3–6 months; García-París *et al.*, 2004). The larvae of *P. waltl* can reach very large sizes in the final stages of development (total length up to 109.3 mm), having increased their size five-fold during development (Escoriza & Ben Hassine, 2017). The diet of larvae of *P. waltl* has previously been investigat-

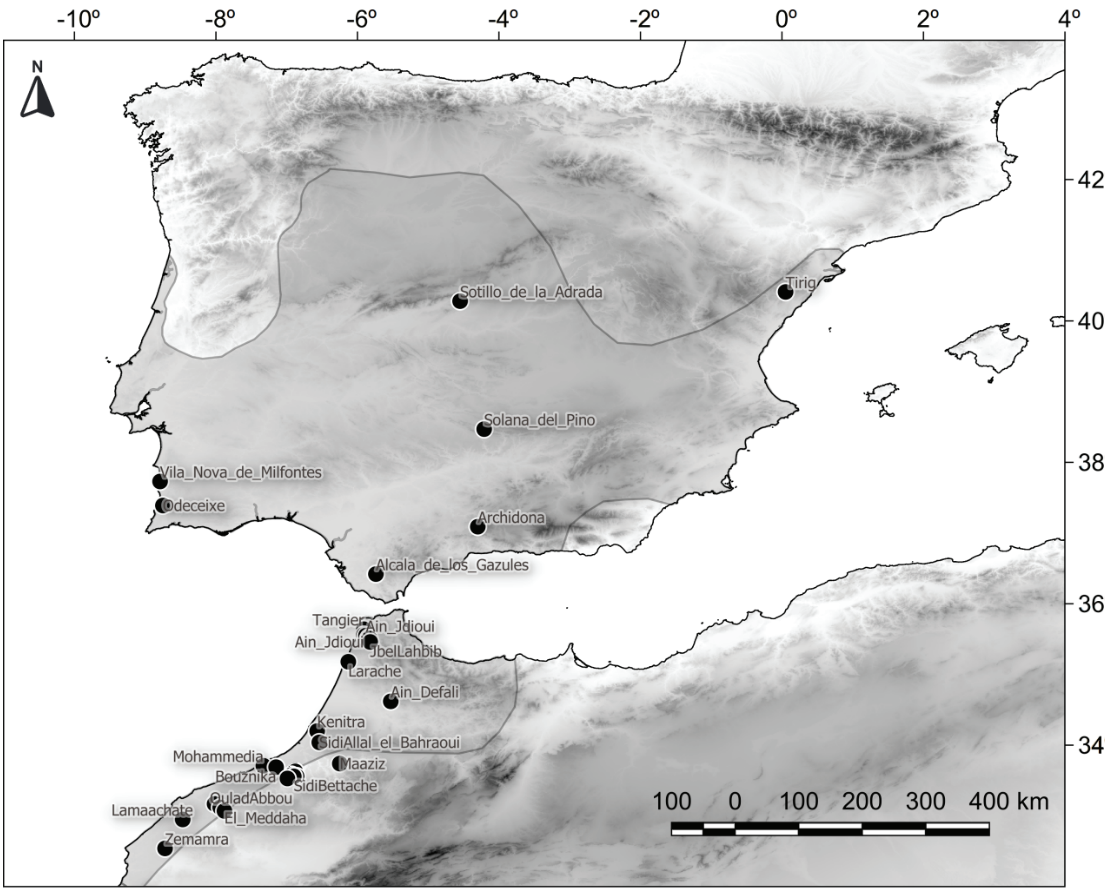

Figure 1. Sampling localities (black circles). The geographic distribution of *Pleurodeles waltl* according to the IUCN (2014) was superimposed. *Localidades de muestreo (círculos negros). El área de distribución de* Pleurodeles waltl*, según la UICN (2014), se muestra superpuesta.*

ed by Díaz-Paniagua (1983) in Doñana, Rodríguez-Jímenez (1985, 1988) in Badajoz, Santos *et al.* (1986) in León and García-de-Lomas *et al.* (2012) in Cádiz. However, these studies were restricted to small geographical areas in Spain, so may have underestimated the trophic range of the species. Other studies of the diet of aquatic urodeles have indicated variability depending on the type of pond and the geographical region (Whiles *et al.*, 2004; Kutrup *et al.*, 2005). For this reason we investigated the diet of *P. waltl* larvae over the entire geographical range of the species, and over a gradient of pond sizes. We aimed to investigate: (i) the type of prey on which the larvae predate and if there is geographical variation in the items found within the stomach contents, and (ii) whether there is qualitative and quantitative variation (type and diversity) in the prey during larval development.

MATERIALS AND METHODS

Sampling and sample processing

Sampling was conducted in February-May 2010 and March 2013, and included most of the breeding season for *P. waltl* (García-París *et al.*, 2004; Escoriza & Ben Hassine, 2015). We surveyed 30 water bodies, having a gradient of surface sizes (91−261 888 m^2) in Spain, Portugal and Morocco; the sites encompassed the complete distributional range of the species (Fig. 1). Except in three localities (Tirig, Solana del Pino and Odeceixe; Table 1) which were watering holes, the sampled water bodies were temporary ponds. The surveying effort was focused on these aquatic habitats because are the most frequently used by *P. waltl* to reproduce (98 % in Morocco; Ben Hassine & Escoriza, 2014). Aquatic habitats were characterized by various chemical parameters: dissolved oxygen (mg/l), pH, and conductivity (µS/cm), and percentage of emergent vegetation cover, which have been shown useful discerning the species composition of communities of aquatic invertebrates (e.g. Van den Berg *et al.*, 1997). Chemical water parameters were measured in situ using a Crison 524 conductivity meter (for conductivity), an EcoScan ph6 (for pH), and a Hach HQ10 Portable LDO meter (for dissolved oxygen). Larvae were captured from all available pond meso-habitats using a net having a mesh size of 250 µm. Five specimens of those captured in each pond were randomly selected for the study. After capture the larvae were anesthetized and fixed in situ in 70 % ethanol. Following return to the laboratory the snout vent and total lengths of each larva were measured to the nearest 0.01 mm using a digital calliper. The stomach was removed from each specimen, and the contents were spread in a Petri dish; posteriorly the prey items were separated, identified and quantified using a stereomicroscope. Macroinvertebrates were classified according their ontogenetic stage (larva/adult) and to family or subfamily level. Microcrustaceans were classified in Daphniidae, Chydoridae, Copepoda and Ostracoda (based on Alonso, 1996, and Tachet *et al.*, 2000). We grouped as a single prey item several Arthropoda fragments found within a stomach if we found also a recognizable head-exoskeleton of the same taxa with some appendages missing. Total lengths were also measured, using approximately 10 intact specimens randomly selected from different samples. The relative abundance of each taxonomic group in a single stomach was used to calculate the frequency of occurrence (FO) and the diversity of prey items using Shannon-Wiener index (Shannon & Weaver, 1962). The frequency of occurrence of the food types was calculated using the formula FO = (S*100)/N where S is the number of stomachs with that food type and N is the total number of stomachs sampled (Loveridge & Macdonald, 2003).

Analyses

We first assessed the extent to which the food items found represent the entire dietary range of the larvae of *P. waltl*. To do this we calculated sample-based rarefaction curves and the 95 % confidence intervals (Colwell *et al.*, 2004), using the Paleontological Statistics package (PAST; Hammer, 2015).

Geographic variation of the diet of *P. waltl* larvae was evaluated by a PERMANOVA test (one fixed factor with two categories, Morocco and Iberian Peninsula), based on the Bray-Curtis distance matrix (Clarke & Gorley, 2006). To evaluate variation in the diet throughout larval development, we investigated whether there were significant differences among arbitrary size groups (Whiles *et al.*, 2004): small-sized (SVL 9.8–22.0 mm, mean = 17.7 mm, n = 66), medium-sized (SVL 22.1–29.6 mm, mean = 25.4 mm, n = 45) and large-sized (SVL 30.2–52.0 mm, mean = 35.8 mm, n = 39). To do this we conducted a PERMANOVA test using the Bray-Curtis distance matrix, including log(pond area), percentage of emergent vegetation, pH, conductivity and dissolved oxygen as covariates. The relationship between the snout-vent length (SVL) and item abundance (or number of total items in the stomach content) and diversity (Shannon Wiener index) was established using a distance-based linear model (Clarke & Gorley, 2006). To determine whether the predictors exerted a positive or negative influence on the dependent variable, we generated XY scatter plots using trend lines. These analyses were performed using the packages PAST and PRIMER-e vs. 6.0 (PRIMER-e Ltd, Plymouth).

Table 1. Sampling localities: country, locality name (municipality), coordinates (geodetic datum = WGS84), elevation, pond surface area (in m^2), and SVL mean and range (*Pleurodeles* larvae snout-vent length, in mm). *Localidades de muestreo: país, nombre de la localidad (municipio), coordenadas (datum geodético = WGS84), altitud, superficie de la charca (en m^2) y media y rango de SVL (longitud hocico-cloaca de las larvas de* Pleurodeles*, en mm).*

Country	Locality	Latitude	Longitude	Elevation (m a.s.l)	Pond area (m^2)	SVL-mean (range)
Spain	Tirig	40.41	0.05	480	169	17.0 (14.8-19.7)
Spain	Sotillo de la Adrada	40.28	-4.55	760	91	16.9 (14.9-21.6)
Spain	Solana del Pino	38.47	-4.21	761	468	24.2 (15.6-34.3)
Portugal	Vila Nova de Milfontes	37.73	-8.79	25	3960	22.3 (17.7-27.3)
Portugal	Odeceixe	37.39	-8.75	117	520	20.9 (15.1-32.6)
Spain	Archidona	37.09	-4.30	812	14 280	26.9 (19.3-38.7)
Spain	Alcalá de los Gazules	36.42	-5.74	56	504	23.2 (19.5-29.1)
Morocco	Tangier	35.64	-5.91	2	261 888	18.0 (14.5-23.9)
Morocco	Ain Jdioui	35.56	-5.91	3	26 395	22.9 (9.8-31.0)
Morocco	Ain Jdioui	35.55	-5.88	5	33 240	26.9 (21.8-41.4)
Morocco	Ain Jdioui	35.52	-5.84	11	175	22.0 (14.7-39.0)
Morocco	Dar Chaoui	35.51	-5.83	46	2348	19.2 (13.0-23.0)
Morocco	Jbel Lahbib	35.46	-5.82	18	1984	29.1 (15.0-46.3)
Morocco	Larache	35.18	-6.13	2	12 345	26.5 (19.0-39.8)
Morocco	Ain Defali	34.62	-5.53	92	5431	29.0 (21.9-35.7)
Morocco	Kenitra	34.20	-6.57	103	1340	27.5 (21.7-33.3)
Morocco	Sidi Allal el Bahraoui	34.04	-6.54	161	2775	27.5 (20.0-30.9)
Morocco	Maaziz	33.74	-6.25	369	10 239	33.9 (17.6-45.4)
Morocco	Mohammedia	33.71	-7.33	36	1417	32.9 (19.3-52.0)
Morocco	Bouznika	33.69	-7.15	183	2530	20.7 (16.8-24.4)
Morocco	Sidi Bettache	33.63	-6.88	369	4840	19.0 (13.8-28.8)
Morocco	Sidi Bettache	33.58	-6.93	387	455	28.9 (21.8-32.3)
Morocco	Sidi Bettache	33.56	-6.86	416	787	22.1 (18.0-29.4)
Morocco	Sidi Bettache	33.56	-6.90	409	10 283	32.1 (29.6-33.6)
Morocco	Souk El Had Frid	33.53	-6.99	354	27 714	21.9 (16.3-26.8)
Morocco	Oulad Abbou	33.17	-8.02	199	7630	22.1 (12.8-30.9)
Morocco	Oulad Abbou	33.12	-7.94	216	7125	27.5 (13.4-34.1)
Morocco	El Meddaha	33.07	-7.88	272	1557	28.1 (20.4-34.8)
Morocco	Lamaachate	32.95	-8.47	113	358	34.0 (27.8-43.3)
Morocco	Zemamra	32.54	-8.72	16	2201	19.1 (14.7-29.0)

RESULTS

We collected 150 larvae in 30 aquatic habitats (temporary ponds and watering holes, Table 1). The aquatic habitats mean surface was 14 775 m^2 ± 3824 standard error (SE) and the water of these habitats showed the following values: dissolved oxygen mean = 7.75 mg/l ± 0.25 SE, pH mean = 8.10 ± 0.05 SE, conductivity mean = 657.7 µS/cm ± 82.5 SE and percentage of emergent vegetation cover 64 % ± 2.3 SE. The larvae had total lengths ranging from 18.7 to 90.9 mm (SVL 9.8–52.0 mm). All captured larvae showed several food items in the stomach contents. In general, we found a total of 33 taxa in the 150 larval stomachs, including benthic invertebrates, terrestrial Arthropoda, and other amphibian larvae.

The analysis showed that the larvae fed mainly

Table 2. Taxa found in the stomach of the larvae: size (axial length range, in mm), *n* (number of items found), Ocurrence % (frequency of occurrence) and SVL mean and range (*Pleurodeles* larvae snout-vent length, in mm). Asterisks indicate non-aquatic groups. [1]Not including Hydroporinae larvae. *Taxones encontrados en el estómago de las larvas: tamaño (rango de longitud axial, en mm), ocurrencia % (frecuencia de ocurrencia) y media y rango de SVL (longitud hocico-cloaca de las larvas de* Pleurodeles*, en mm). Los asteriscos indican grupos no acuáticos. [1]Sin incluir larvas de Hydroporinae.*

Taxon	Size	*n*	Ocurrence%	SVL mean(range)
Daphniidae	0.5-1.0	4102	86.7	24.9 (13.0-52.0)
Ostracoda	0.5-1.0	2577	89.3	25.1 (9.8-52.0)
Chydoridae	0.5	2080	86.0	24.7 (12.8-52.0)
Copepoda	1.0	1518	78.0	25.2 (9.8-52.0)
Chironomidae (larvae)	2.0-4.0	657	57.3	26.0 (9.8-52.0)
Culicidae (larvae)	5.0-6.0	80	8.0	23.7 (13.8-32.8)
Dytiscidae[1] (larvae)	7.0-9.0	77	30.0	29.9 (12.8-52.0)
Homoptera*	3.0	43	2.7	23.9 (17.7-29.4)
Diptera (adults)*	2.0-5.0	38	14.7	30.2 (16.4-46.3)
Ephemeroptera (larvae)	2.0-4.0	26	10.0	29.8 (15.0-45.6)
Anostraca	5.0-9.0	23	6.0	31.4 (23.6-34.3)
Ephydridae (larvae)	1.0-4.0	23	4.7	30.4 (23.0-34.8)
Anura (larvae)	10.0-19.0	11	6.0	35.0 (22.0-52.0)
Planorbidae	3.0-6.0	11	1.3	30.0 (29.6-30.5)
Physidae	4.0-5.0	10	4.0	25.1 (17.1-39.0)
Spinicaudata	2.0-5.0	10	2.7	31.8 (28.8-33.6)
Nematoda	1.0-2.5	9	3.3	21.6 (14.9-30.2)
Ceratopogonidae (larvae)	2.0-5.0	8	4.0	27.4 (17.5-37.8)
Hydroporinae	3.0-4.0	7	3.3	34.2 (22.7-52.0)
Hydrophilidae (larvae)	3.0-6.0	7	4.0	28.2 (21.0-39.0)
Sminthuridae*	2.0	7	4.0	27.4 (16.3-34.1)
Corixidae (adults)	3.0-10.0	7	4.0	34.2 (21.6-52.0)
Corixidae (larvae)	2.0-5.0	5	2.0	20.0 (16.9-22.4)
Libellulidae (larvae)	10.0-15.0	3	2.0	40.6 (37.8-43.3)
Acari	2.0-3.0	2	0.7	29.6
Vegetal matter	4.0-6.0	2	1.3	26.1 (21.2-31.1)
Salamandridae (larvae)	10.0	1	0.7	39.8
Dytiscidae (adults)	11.0	1	0.7	32.2
Notonectidae (adults)	12.0	1	0.7	33.3
Haliplidae (adults)	3.0	1	0.7	32.6
Formicidae*	7.0	1	0.7	35.7
Staphylinidae*	6.0	1	0.7	33.3
Asellidae	2.0	1	0.7	24.0

on microcrustaceans (Cladocera, Ostracoda and Copepoda) and larvae of aquatic Insecta (Table 2). The rarefaction curve tended to stabilize, suggesting that these taxa represented a large part of the larval diet (Fig. 2). The PERMANOVA test showed significant differences in the item abundance comparing the samples from Iberian Peninsula and Morocco (df = 1, pseudo–F = 3.78, *P* = 0.0005). The PERMANOVA test also showed significant differences in the stomach contents among the three size groups (df = 2, pseudo–F = 2.69, *P* = 0.0003), without these differences being affected by chemical parameters (size groups x dissolved oxygen, pseudo–F = 1.18, *P* = 0.275; size groups x pH, pseudo–F = 1.34, *P* = 0.154; size groups x conductivity, pseudo–F = 0.99, *P* = 0.460) or percentage of emergent cover vegetation (pseudo–F = 1.18, *P* = 0.271) but by the size of the water body (pseudo–F = 2.69, *P* = 0.0006).

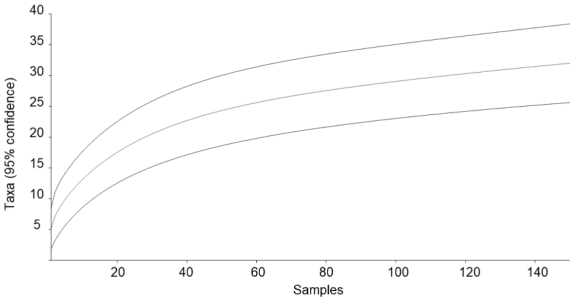

Figure 2. Rarefaction curves (shown with 95 % confidence intervals) for the number of taxa that are expected as a function of sampling effort from the stomach content. *Curvas de rarefacción (que se muestran con intervalos de confianza del 95 %) para el número de taxones que se esperan en función del esfuerzo de muestreo del contenido del estómago.*

The distance-based linear model indicated that the differences were attributable to the higher frequency of large-sized taxa in the digestive tract of larvae in advanced stages, including Anuran and Dytiscidae larvae and adult specimens of Diptera and Corixidae (Fig. 3 and Table 3). This dietary diversification in the advanced larval phases also produced a positive and

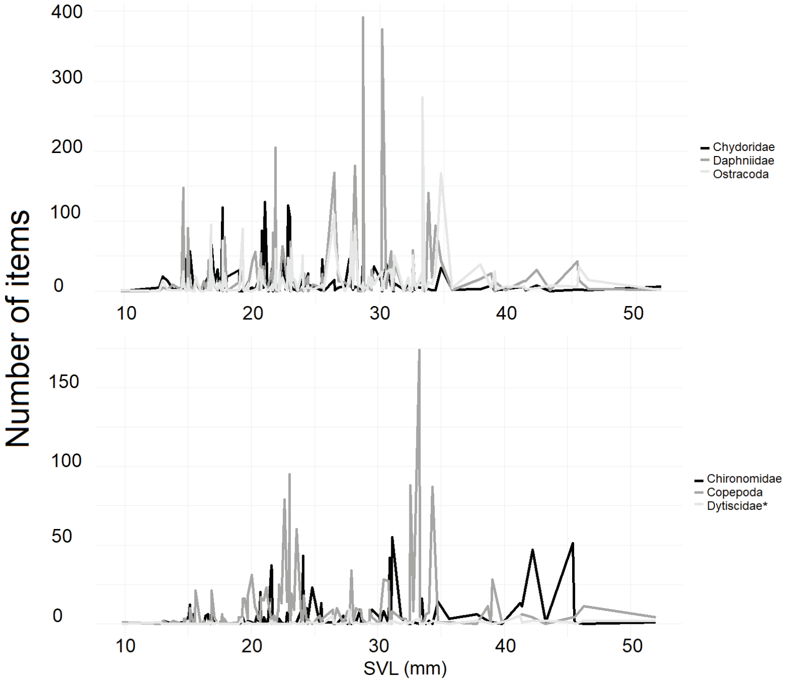

Figure 3. Relationship between the size of the larvae (SVL) of *Pleurodeles waltl* and the number of prey items in the stomach contents for the most prevalent taxa (FO ≥ 30%). Dytiscidae*, larvae. *Relación entre el tamaño de las larvas (SVL) de* Pleurodeles waltl *y el número de presas en el contenido estomacal para los taxones más prevalentes (FO ≥ 30 %). Dytiscidae*, larvas.*

Table 3. Results of the distance-based linear model assessing the relationship between the larvae SVL and item abundance. [1]Not including Hydroporinae larvae. Only the statistically significant associations are shown. +/− indicates the sense (positive or negative) of the associations. Proportion, proportion of explained variance; P, probability level. *Resultados del modelo lineal basado en las distancias que evalúa la relación entre la SVL de larvas y la abundancia de ítems. [1]Sin incluir larvas de Hydroporinae. Sólo se muestran las asociaciones estadísticamente significativas. +/− indica el sentido (positivo o negativo) de las asociaciones. Proporción, proporción de varianza explicada; P, nivel de probabilidad.*

Taxon	+/-	Pseudo-F	*P*	Proportion
Chydoridae	-	4.68	0.034	0.031
Chironomidae(larvae)	+	7.68	0.007	0.049
Dytiscidae[1] (larvae)	+	18.82	0.0001	0.113
Diptera (adults)	+	12.34	0.0007	0.077
Ephemeroptera (larvae)	+	4.56	0.030	0.029
Anura (larvae)	+	19.01	0.0001	0.114
Hydroporinae	+	13.24	0.001	0.082
Corixidae (adults)	+	8.81	0.004	0.056
Libellulidae (larvae)	+	8.00	0.011	0.051

statistically significant association between the SVL and prey item diversity (Pseudo-F = 21.67, $P = 0.001$).

DISCUSSION

In this study we found that the larvae of *P. waltl* are important predators of microcrustaceans, as reported previously by Díaz-Paniagua *et al*. (2005) and García-de-Lomas *et al.* (2012). However, larvae preyed on a very broad spectrum of other aquatic invertebrates, including insect larvae (Chironomidae, Culicidae, Dytiscidae and Ephemeroptera), Gastropoda (also previously indicated by Rodríguez-Jiménez, 1985 and Santos *et al.*, 1986), and non-aquatic Arthropoda (Homoptera, Sminthuridae). Amphibian larvae (including conspecifics) were also present, but in our samples cannibalism was exceptional (0.7 %). This finding contrasts with those obtained in other diet studies that have reported that cannibalism is common among urodele larvae (Wildy *et al.*, 2001; Vaissi & Sharifi, 2016). This may be because our surveys were conducted during early and mid-spring, when many of the ponds sampled were at the beginning of the drying phase. It is possible that cannibalism increases during the terminal phases of the hydroperiod, when the larval density also increases (Lannoo & Bachmann, 1984), but this hypothesis remains to be tested.

The analyses also revealed a geographical structure in the diet composition (i.e. differences between the Iberian Peninsula and Morocco), which could be attributed to the variation in the invertebrate communities between both regions (Escoriza *et al.*, 2016). The items found in the digestive tract showed that *P. waltl* larvae forage at both the water surface (suggested by the presence of non-aquatic Arthropoda and adult Diptera) and close to the benthos (suggested by the presence of benthic and periphytic taxa, including Chydoridae, Ostracoda and Chironomidae larvae). The latter taxa are common in or near the bottom substrate in ponds (Francis & Kane, 1995; Sacherová & Hebert, 2003; Kotov, 2006; Martens *et al.*, 2008). Therefore our study demonstrates that *P. waltl* larvae feed on several types of animal prey and use a range of pond meso-habitats.

Our analyses also showed that the prey items were influenced by larval size and pond area, although larvae of all sizes preyed intensely on microcrustaceans (Branchiopoda, Ostracoda and Copepoda). The effect of the water body size on the composition of the lentic invertebrate communities is well known (Batzer *et al.*, 2004) and can be expected to have influence on the diet. We found a positive correlation between larval size, item diversity and the abundance of moderate/large sized insect larvae (Chironomidae, Dytiscidae, Libellulidae and Ephemeroptera), adult forms of aquatic insects (Corixidae) and Anura larvae. This indicates that there was no major ontogenetic change in the diet of *P. waltl* larvae, but it diversified on larger prey during advanced developmental stages. Similar conclusions were reached by Diaz-Paniagua (1983) in Doñana, Santos *et al.* (1986) in León and Rodríguez-Jiménez (1988) in Badajoz.

Our results are also consistent with previous studies on the diet of other species of pond-dwelling urodele larvae, and highlight the importance of swimming-type microcrustaceans (e.g. daphniids; Hutcherson *et al.*, 1989) to this larval guild. By contrast, stream-dwelling larvae typically predate on benthic Insecta (Chironomidae and Ephemeroptera larvae) and bivalves (Sphaeriidae) (Parker, 1994; Cecala *et al.*, 2007). These findings may reflect distinct predatory patterns (urodele larvae inhabiting streams remain closely attached to the substrate; Petranka, 1998), but also prey availability, because swimming-type microcrustaceans are rare in streams with high water velocities (Ebert, 2005).

Overall, our findings suggest that suitable breeding habitats for *Pleurodeles* species need to contain abundant microcrustaceans and insect larvae. This could explain its population decrease or extinction in aquatic habitats where predatory fish (e.g. *Gambusia*) have been introduced (Ben Hassine *et al.*, 2016), because these can completely remove aquatic microcrustaceans (Hurlbert *et al.*, 1972). This suggests that eliminating predatory alien fish from aquatic habitats should be a priority when managing endangered populations of *Pleurodeles*, including reintroduction of captive-bred specimens (Jiménez & Lacomba, 2002).

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REFERENCES

ALONSO, M. 1996. *Crustacea. Branchiopoda*. Museo Nacional de Ciencias Naturales-CSIC. Madrid. Spain.

BATZER, D. P., B. J. PALIK & R. BUECH. 2004. Relationships between environmental characteristics and macroinvertebrate communities in seasonal woodland ponds of Minnesota. *Journal of the North American Benthological Society*, 23: 50–68. DOI: 10.1899/0887-3593(2004)023<0050:RBECAM>2.0.CO;2

BEN HASSINE, J. & D. ESCORIZA. 2014. New ecological data on the family Salamandridae in the Maghreb. *Herpetological Review*, 45: 193–200.

BEN HASSINE, J., D. ESCORIZA & B. BAKHOUCHE. 2016. Factors determining the occurrence of *Pleurodeles poireti* (Caudata: Salamandridae) on Edough Peninsula, northeastern Algeria. *African Journal of Herpetology*, 65: 55–67. DOI: 10.1080/21564574.2016.1167783

CECALA, K. K., S. J. PRICE & M. E. DORCAS. 2007. Diet of larval red salamanders (*Pseudotriton ruber*) examined using a nonlethal technique. *Journal of Herpetology*, 41: 741–745. DOI: 10.1670/07-019.1

CLARKE, K. R. & R. N. GORLEY. 2006. PRIMER v6: User Manual/Tutorial. PRIMER–E Ltd. Plymouth. UK.

COLWELL, R. K., C. X. MAO & J. CHANG. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85: 2717–2727. DOI: 10.1890/03-0557

DAVIC, R. D. 1991. Ontogenetic shift in diet of *Desmognathus quadramaculatus*. *Journal of Herpetology*, 25: 108–111. DOI: 10.2307/1564806

DÍAZ-PANIAGUA, C. 1983. Notas sobre la alimentación de larvas de anfibios: 1. *Pleurodeles waltl* en charcas temporales. *Doñana, Acta Vertebrata*, 10: 204–207.

DÍAZ-PANIAGUA, C., C. GÓMEZ-RODRÍGUEZ, A. PORTHEAULT & W. DE VRIES. 2005. *Los Anfibios de Doñana*. Organismo Autónomo de Parques Nacionales. Ministerio de Medio Ambiente. Madrid. Spain.

DURANT, S. E. & W. A. HOPKINS. 2008. Amphibian predation on larval mosquitoes. *Canadian Journal of Zoology*, 86: 1159–1164. DOI: 10.1139/Z08-097

EBERT, D. 2005. *Ecology, epidemiology, and evolution of parasitism in Daphnia*. National Library of Medicine (US), National Center for Biotechnology Information. Bethesda. USA.

ESCORIZA, D. & J. BEN HASSINE. 2015. Niche partitioning at local and regional scale in the North African Salamandridae. *Journal of Herpetology*, 49: 276–283. DOI: 10.1670/13-151

ESCORIZA, D., J. BEN HASSINE, J. SALA

& D. BOIX. 2016. Zoophagy in the larvae of Ibero-Maghrebian spade-foot toads. *Herpetologica*, 72: 281–287. DOI: 10.1655/HERPETOLOGICA-D-16-00001.1

ESCORIZA, D. & J. BEN HASSINE. 2017. Comparative larval morphology in three species of *Pleurodeles* (Urodela: Salamandridae). *Zootaxa*, 4237: 587–592. DOI: 10.11646/zootaxa.4237.3.11

FRANCIS, D. R. & T. C. KANE. 1995. Effect of substrate on colonization of experimental ponds by Chironomidae (Diptera). *Journal of Freshwater Ecology*, 10: 57–63. DOI: 10.1080/02705060.1995.9663417

GALIEN, L. & M. DUROCHER. 1957. Tables de développement chez *Pleurodeles waltl*. *Bulletin Biologique de la France et de la Belgique*, 91: 97–117.

GARCÍA-DE-LOMAS, J., J. M. TORRES, R. REQUES & I. HERNÁNDEZ. 2012. *Pleurodeles waltl* newt larvae diet regarding available prey: Choice or mere coincidence?. *Copeia*, 2012: 756–761. DOI: 10.1643/CE-11-032

GARCÍA-PARÍS, M., A. MONTORI & P. HERRERO. 2004. *Fauna Ibérica, Amphibia: Lissamphibia*. Museo Nacional de Ciencias Naturales-CSIC. Madrid. Spain.

HAMMER, Ø. 2015. PAST: PAleontologicalSTatistics software package, v3.06. Available at http://nhm2.uio.no/norlex/past/download.html

HOLOMUZKI, J. R. & J. P. COLLINS. 1987. Trophic dynamics of a top predator, *Ambystoma tigrinum nebulosum* (Caudata: Ambystomatidae), in a lentic community. *Copeia*, 1987: 949−957. DOI: 10.2307/1445558

HURLBERT, S. H., J. ZEDLER & D. FAIRBANKS. 1972. Ecosystem alteration by mosquito fish (*Gambusia affinis*) predation. Science, 175: 639–641. DOI: 10.1126/science.175.4022.639

HUTCHERSON, J. E., C. L. PETERSON & R. F. WILKINSON. 1989. Reproductive and larval biology of *Ambystoma annulatum*. *Journal of Herpetology*, 23: 181−183. DOI: 10.2307/1564028

INTERNATIONAL UNION FOR CONSERVATION OF NATURE (IUCN). 2014. The IUCN Red List of Threatened Species. Available at http://www.iucnredlist.org.

JIMÉNEZ, J. & J. I. LACOMBA. 2002. La conservación de la herpetofauna valenciana. *Revista Española de Herpetología*, 2002: 111−117.

KOTOV, A. A. 2006. Adaptations of Anomopoda crustaceans (Cladocera) to the benthic mode of life. *Entomological Review*, 86: S210-S225. DOI: 10.1134/S0013873806110157

KUSANO, T., H. KUSANO & K. MIYASHITA. 1985. Size-related cannibalism among larval *Hynobius nebulosus*. *Copeia*, 1985: 472−476. DOI: 10.2307/1444861

KUTRUP, B., E. ÇAKIR & N. YILMAZ. 2005. Food of the banded newt, *Triturus vittatus ophryticus* (Berthold, 1846), at different sites in Trabzon. *Turkish Journal of Zoology*, 29: 83−89.

LANNOO, M. J. & M. D. BACHMANN. 1984. Aspects of cannibalistic morphs in a population of *Ambystoma t. tigrinum* larvae. *American Midland Naturalist*, 112: 103−109. DOI: 10.2307/2425463

LOVERIDGE, A. J. & D. W. MACDONALD. 2003. Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). *Journal of Zoology*, 259: 143–153. DOI: 10.1017/S0952836902003114

MARTENS, K., I. SCHÖN, C. MEISCH & D. J. HORNE. 2008. Global diversity of ostracods (Ostracoda, Crustacea) in freshwater. *Hydrobiologia*, 595: 185–193. DOI: 10.1007/s10750-007-9245-4

PARKER, M. S. 1994. Feeding ecology of stream-dwelling Pacific giant salamander larvae (*Dicamptodon tenebrosus*). *Copeia*, 1994: 705–718. DOI: 10.2307/1447187

PETRANKA, J. W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press. Washington DC. USA.

RODRÍGUEZ-JIMÉNEZ, A. J. 1985. Competencia trófica entre *Pleurodeles waltl* y *Triturus marmoratus* (Amphibia, Caudata) durante su desarrollo larvario en cursos fluviales temporales. *Alytes*, 3: 21–30.

RODRÍGUEZ–JIMÉNEZ, A. J. 1988. Fenología de una comunidad de anfibios asociada a cursos fluviales temporales. *Doñana, Acta Vertebrata*, 15: 29−43.

SACHEROVÁ, V. & P. D. N. HEBERT. 2003.

The evolutionary history of the Chydoridae (Crustacea: Cladocera). *Biological Journal of the Linnean Society*, 79: 629–643. DOI: 10.1046/j.1095-8312.2003.00216.x

SANTOS, F. J., A. SALVADOR & C. GARCÍA. 1986. Dieta de larvas de *Pleurodeles waltl* y *Triturus marmoratus* (Amphibia: Salamandridae) en simpatría en dos charcas temporales de León. *Revista Española de Herpetología*, 1: 295–313.

SHANNON, C. & W. WEAVER. 1962. The Mathematical Theory of Communication. University of Illinois Press. Urbana.

TACHET, H., P. RICHOUX, M. BOURNAUD & P. USSEGLIO-POLATERA. 2000. *Invertébrés d'Eau Douce: Systématique, Biologie, Écologie* (Vol. 15). CNRS. Paris. France.

VAISSI, S. & M. SHARIFI. 2016. Variation in food availability mediate the impact of density on cannibalism, growth, and survival in larval yellow spotted mountain newts (*Neurergus microspilotus*): Implications for captive breeding programs. *Zoo Biology*, 35: 513−521. DOI: 10.1002/zoo.21327

VAN DEN BERG, M. S., H. COOPS, R. NOORDHUIS, J. VAN SCHIE & J. SIMONS. 1997. Macroinvertebrate communities in relation to submerged vegetation in two Chara-dominated lakes. *Hydrobiologia*, 342: 143–150. DOI: 10.1023/A:1017094013491

WELLS, K. D. 2010. *The Ecology and Behavior of Amphibians*. University of Chicago Press. Chicago and London. USA.

WHILES, M. R., J. B. JENSEN, J. G. PALIS & W. G. DYER. 2004. Diets of larval flatwoods salamanders, *Ambystoma cingulatum*, from Florida and South Carolina. *Journal of Herpetology*, 38: 208–214. DOI: 10.1670/124-03N-A

WHITEMAN, H. H., S. A. WISSINGER & W. S. BROWN. 1996. Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum*. *Evolutionary Ecology*, 10: 433–446. DOI: 10.1007/BF01237728

WILDY, E. L., D. P. CHIVERS, J. M. KIESECKER & A. R. BLAUSTEIN. 2001. The effects of food level and conspecific density on biting and cannibalism in larval long-toed salamanders, *Ambystoma macrodactylum*. *Oecologia*, 128: 202−209. DOI: 10.1007/s004420100641

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