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POPULATION ECOLOGY - ORIGINAL RESEARCH

Intercohort size structure dynamics of fire salamander larvae in ephemeral habitats: a mesocosm experiment

Asaf Sadeh[1,2] · Antonina Polevikov[1] · Marc Mangel[3,4] · Leon Blaustein[1]

Abstract The size structure of a larval population facilitates interaction asymmetries that, in turn, influence the dynamics of size-structure. In species that exhibit conspicuous aggressive interactions, the competitive effects of the smaller individuals may be overlooked. We manipulated initial size differences between two larval cohorts and young-cohort density of *Salamandra infraimmaculata* in mesocosms to determine: (1) whether young individuals function primarily as prey or as competitors of older and larger individuals; (2) the resulting dynamics of size variation; and (3) recruitment to the postmetamorph population. Intercohort size differences generally remained constant over time at low young-cohort densities, but reduced over time at high densities due to retardation of the old-cohort growth rate. This suggests a competitive advantage to the young cohort that outweighs the interference advantage of older cohorts previously documented in this species. The increase in mortality from desiccation due to high young-cohort density was an order of magnitude greater in the old cohort than in the young-cohort, further indicating size-dependent vulnerability to competition. However, the conditions least favorable to most of the old-cohort larvae (large size difference and high young-cohort density) promoted cannibalism. Among cannibals, mortality and time to metamorphosis decreased and sizes at metamorphosis increased substantially. Thus, a balance between the competitive advantage to young cohorts, and the interference and cannibalism advantage to old cohorts shapes larval size-structure dynamics. Larval densities and individual expression of cannibalism can shift this balance in opposite directions and alter relative recruitment rates from different cohorts.

Keywords Amphibians · Exploitative competition · Fire salamander · Niche shifts · Priority effects

Introduction

Asymmetric interactions among members of structured populations may affect life histories (De Block and Stoks 2004; Sadeh et al. 2009) and lead to complex population-level patterns (Claessen et al. 2004). Size structure is a universal source of interaction asymmetries, including asymmetric competition for food resources, aggressive interference, and cannibalism. In organisms with complex life cycles that use temporary larval habitats, time constraints on larval development (Loman 2002; Sadeh et al. 2011) exacerbate the effects of such consumption-modifying factors. Therefore, size structure can be important for larval performance and the resulting recruitment patterns to the adult population (Wissinger et al. 2010). Theory suggests that the outcome of the combination of competition and cannibalism depends crucially on each of the two components of size structure: the size differences between

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✉ Asaf Sadeh
asaffield@gmail.com

1 Department of Evolutionary and Environmental Biology and the Institute of Evolution, Faculty of Natural Sciences, University of Haifa, 31905 Haifa, Israel

2 Present Address: Department of Entomology, Hebrew University of Jerusalem, Rehovot, Israel

3 Department of Applied Mathematics and the Center for Stock Assessment, University of California, Santa Cruz, CA 95064, USA

4 Department of Biology, University of Bergen, Bergen, Norway

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size classes, and the distribution of individuals among them (Huss et al. 2010).

Initial size variation can be caused by variation in size at birth, and by the pattern of colonization by larval cohorts (e.g., Anholt 1994; Hopper et al. 1996; Eitam et al. 2005; Sadeh et al. 2009). Once an initial size variation is generated, the size differences between cohorts can increase, diminish or remain constant over time. Size differences can increase if the smaller members of young cohorts are excluded access to food resources by the older cohorts through aggressive interference (Ziemba and Collins 1999; Ziemba et al. 2000; Preisser et al. 2005). Cannibalism results in energy transfer between cohorts and, at sufficiently high rates, can lead to further size divergence (Huss et al. 2010). On the other hand, the growth rates of many organisms diminish with body size (Persson 1985; Werner 1994), resulting in a potential for small individuals to catch up in size to larger conspecifics and thus to reduce the potential for cannibalism and other size-biased interactions. The dynamics of intercohort size differences may be important for the emergence and sustenance of size-dependent interactions (Huss et al. 2010), for variation in life histories and behaviors (Polis 1988), and for within-season recruitment patterns (Huss et al. 2008a).

Exploitative competition, interference, and cannibalism are all also strongly density-dependent. Higher densities of young cohorts relative to those of the older cohorts may facilitate increased cannibalism rates. On the other hand, the strength of exploitative competition that young cohorts potentially exert on older, larger cohorts may be significant (Persson 1985; Polis 1988; Hjelm and Persson 2001). Aggressive behavior can depend on density in a more complex manner (Grant et al. 2002; Kaspersson et al. 2010). Intercohort size dynamics and interactions, particularly the effects of young-cohort densities, have been understudied, probably due to technical difficulties in identifying and following individuals over time, and often due to the conspicuousness of cannibalistic and other aggressive behaviors compared to exploitative competition. These questions can be addressed in the fire salamander system by nonintrusive individual identification of larvae by their tailfin spot pattern (Eitam and Blaustein 2002).

Here, we investigate size-structure dynamics and their consequences using the fire salamander, *Salamandra infraimmaculata* (Steinfartz et al. 2000). Fire salamanders on Mt. Carmel, Israel, breed mostly in temporary pools, some of which hold very small volumes of water (Spencer et al. 2002; Segev and Blaustein 2014). In these pools, cannibalism (Degani 1993; Sadeh 2012) and pool desiccation prior to metamorphosis (Warburg 1992; Sadeh et al. 2011) are considered major sources of mortality. Females spread their larvae both temporally within the

breeding season and spatially among available temporary pools (Segev et al. 2011), leading to the colonization of most pools by sequential cohorts at variable time intervals. The larvae are size-selective, generalist top predators (Blaustein et al. 1996). Previous studies on inter-cohort interactions focused on the effects of older cohort densities on young cohort metamorphic success (Eitam et al. 2005) and on size-dependent cannibalism (Degani et al. 1980; Sadeh et al. 2009). Interference behavior by large individuals towards smaller ones is readily observed among larvae, both in the laboratory and in the field (Sadeh, personal observations).

We conducted a mesocosm experiment in which we manipulated initial larval size structure by varying the time interval between two larval cohorts sharing the same pool and the densities of the smaller cohort. We investigated: (1) whether initial size differences tend to increase, decrease or remain constant with time; (2) whether varying young-cohort densities affect older cohorts as would be expected from conspecific prey or as would be expected from competitors, and whether this depends on their initial size differences; and (3) how these interactions affect the metamorphic success of both cohorts under natural time limitation.

Materials and methods

In an outdoor, factorial experiment conducted on the University of Haifa campus on Mt. Carmel, Israel (elevation 460 m ASL), we crossed three time intervals (which we denote by $\Delta t = 0$, 9 and 22 days) between colonizations by the old and the young larval cohorts with two densities of young cohort larvae (three and six larvae/pool). We replicated each treatment combination nine times and allocated treatments randomly to the 54-mesocosm array.

Mesocosm setup and animal collection

We enclosed the entire outdoor experimental array in chicken wire (mesh size 3 cm) that was mounted on a frame and allowed colonization by most insects but prevented disturbance by domestic animals. Natural pools were simulated in 40-l mesocosms (floor area 0.22 m^2), initially filled with aged tap water. The size of the mesocosms was well within the range of natural pools utilized by salamanders (e.g., as low as 3 l pools; Spencer et al. 2002; Blaustein, personal observations). Initial larval densities were well within the naturally occurring range. For example, a mean density of 0.2 larvae/l was found in an array of rock pools (Segev and Blaustein 2014), and in another site we have observed densities of up to 8 larvae/l (Blaustein, personal

observations). We placed a plastic net (mesh size 1 mm) over the soil, covering the bottom and walls of the mesocosms to the rims. We placed five rocks (each displacing ~150 ml of water) on the plastic net for structural complexity. The net allowed us to easily lift out the salamander larvae during the experiment for rapid and accurate counting and measurement. We attached to the net, on the rims of each mesocosm, a horizontal plastic ledge (5 cm wide) to prevent climbing metamorphs from escaping.

We collected gravid *S. infraimmaculata* females on their way to their natural breeding sites on Mt. Carmel during early winter, 2010, and induced larviposition in the laboratory on days 1, 10 and 23 of the experiment, by placing each of females into a water-filled tub. Upon births, we measured the wet mass of newborn larvae and grouped them according to their maternal origin.

Introduction of larvae to mesocosms

The old cohort consisted of three newborn larvae, placed into each of the 54 mesocosms on day 1 of the experiment (mean individual wet mass 247 mg, SD = 38 mg). We photographed the tailfins of all the old-cohort larvae for individual identification (Eitam and Blaustein 2002) and for discrimination between members of the two cohorts throughout the experiment.

On day 1, we also added an additional group of 3 (low density, 9 replicates) or 6 (high density, 9 replicates) larvae (intercohort time interval $\Delta t = 0$ days) to a total of 18 mesocosms. We refer to this additional group as the 'young cohort' even though at $\Delta t = 0$ days it is of the same age as the old cohort. Initial size variation exists also among larvae of the same age due to variation in body sizes vary at birth. However small they may be, initial size differences between the smaller and larger larvae of the same age might still influence their subsequent interactions. Therefore, for the young cohort at $\Delta t = 0$ days, we selected smaller larvae (mean wet mass 207 mg, SD = 17 mg) than those of the 'old cohort'. To establish the initial size difference between the groups in this treatment, old-cohort larvae were selected randomly from those that were larger than the mean wet mass of all the available larvae across breeding sites. Similarly, larvae for the young cohort were selected randomly from those that were smaller than the mean.

We added a young cohort of 3 larvae or 6 larvae (9 replicates each) to the rest of the mesocosms on day 10 and on day 23 (denoted as $\Delta t = 9$ and $\Delta t = 22$ days, respectively). On day 10, the young larvae that were added weighed 216 mg (SD = 27 mg), while the old cohort in these mesocosms had reached a mean mass of 348 mg (SD = 31 mg). On day 23, the young larvae that were added weighed 254 mg (SD = 51 mg), while the old cohort in these mesocosms had reached a mean mass of 519 mg (SD = 40 mg). Initial intercohort size differences were on the low end of naturally occurring size differences which depend on a wide range of time intervals between rain events and larviposition by females (Sadeh and Blaustein, personal observations).

All three old-cohort larvae in each mesocosm originated from the same, randomly chosen group of larvae, born to females from a single natural breeding site. All the larvae of the young cohort in each mesocosm originated from the same, randomly chosen group of larvae born to females from a different site than that of the old cohort. Previous mark–recapture work (Bar-David et al. 2007) showed that adults can move between sites within that region, to which further support was lent by a population genetic survey (Blank et al. 2013). Therefore, the mixing of cohorts from females that originate from different sites is a natural situation.

Resource availability and water levels

Five days before the experiment began, we added 2.220 kg soil to each mesocosm from a dried temporary pool containing a natural assembly of crustacean resting eggs. On days 8 and 16 of the experiment, we added 120 and 230 ml water, respectively, from a natural pond for algal and bacterial inoculation and also included sweep-netted zooplankton at availabilities similar to those of natural pools. The first inoculate contained predominantly *Ceriodaphnia* spp., while the second contained mostly *Arctodiaptomus similis*, *Ceriodaphnia* and a *Cyzicus* sp. These are common local prey of *Salamandra* (Blaustein et al. 1996; Eitam et al. 2005). By day 43, only sporadic individual *A. similis* could be occasionally observed in any of the mesocosms. Food availability remained visibly low in all mesocosms until the onset of spring (circa day 100 of the experiment), when aquatic insects started ovipositing into the mesocosms (mostly the mosquito *Culiseta longiareolata* and chironomids) or terrestrial insects were trapped in them.

Water levels fluctuated naturally with weather conditions, except for days 18 and 44, when we added aged tap water to all mesocosm such that they reached 50 % of their maximal volume. This was done to prevent the mesocosms from desiccating prematurely and killing all the larvae, as was the fate of some of the natural pools that year, due to a dryer-than-usual early winter period. Rains then persisted late into the spring, resulting in longer than usual hydroperiods both in the field and in our mesocosms. We allowed the mesocosms to dry completely, by day 163, and terminated the experiment. Whenever possible, approaching the end of the experiment, we collected larvae that had not

initiated metamorphosis from recently-dried mesocosms and returned them to the field to reduce unnecessary mortality in this locally endangered species.

Data collection

Throughout the experiment, we followed larval mass gain every 2 or 3 weeks, and their survival at least once per week. We distinguished cases of cannibalism either by direct observation, which may take many hours and up to 1 day, by finding the remains of partly cannibalized larvae (they had no other predators), or by the disappearance of a larva coinciding with the sudden increase in mass of one of its pool mates. This is a reasonable estimation of cannibalism since *S. infraimmaculata* larvae usually attack moving prey, and very rarely practice necrophagy (Sadeh, personal observations). Metamorphosing individuals climbed on the plastic net on the mesocosms' walls, and remained in the crease beneath the ledges that prevented their escape. Once the first metamorphs were found, we visited the mesocosms every 2–3 days to collect and remove all the metamorphs. We recorded the time, mass and SVL at emergence for each metamorph.

Statistical analysis

One mesocosm was excluded from the experiment due to the mortality of most of its larvae immediately following introduction. To determine size structure dynamics, we used ANCOVA, analyzing the effects of density (categorical independent variable) and initial intercohort size differences (covariate) on the development of size difference dynamics by day 94 (i.e., the final–initial intercohort size different). Day 94 was the latest day of data collection before the first event of metamorphosis. Since cannibalism was infrequent, we excluded data from mesocosms that involved cannibalism (one tub in $\Delta t = 9$, low density; two tubs in $\Delta t = 22$, high density).

To analyze the effects of the treatments on the old and the young cohorts' metamorphic success, we used two-way ANOVAs to compare mean mortality, time to and size at metamorphosis. We used log and rank transformations of sizes at metamorphosis of the old and the young cohorts, respectively, to meet ANOVA assumptions. The $\Delta t = 9$ and low larval density treatment combination had no variation in old-cohort mortality. Therefore, we excluded the intermediate intercohort interval level ($\Delta t = 9$) from the analysis and used a 2×2 factorial ANOVA. Upon graphical inspection (see below), the pattern of the $\Delta t = 9$ treatments does not differ from that of the two tested levels. An analysis of the full 3×2 dataset (violating ANOVA assumptions) produced similar results, so we do not present it. The analyses of mortality, time to
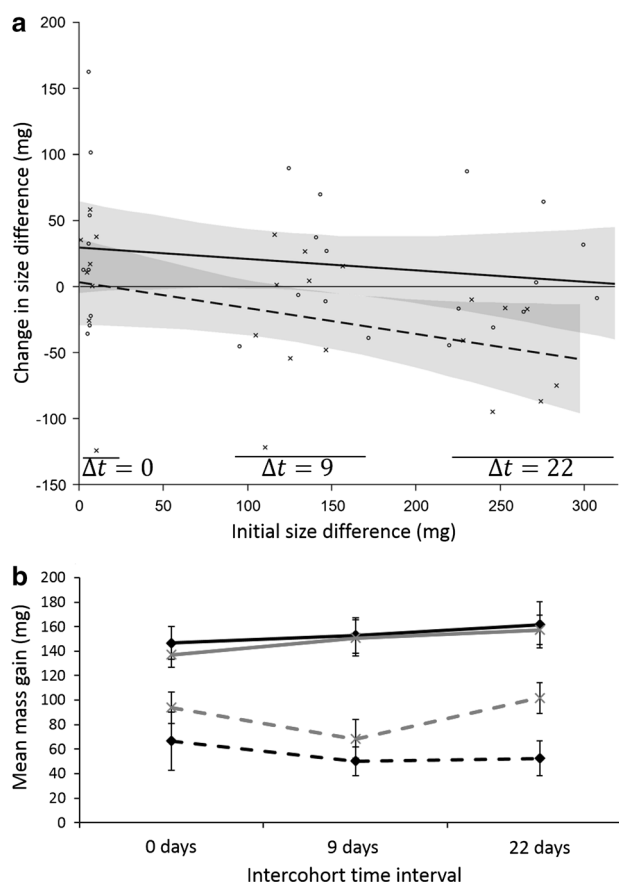

Fig. 1 a Development (cumulative change) of intercohort size difference (old–young cohort) until first metamorphosis as a function of initial intercohort size differences and young-cohort density. *Circles* and *solid regression line* are for low young-cohort densities. *Crosses* and *dashed regression line* are for high young-cohort densities. *Shaded bands* are 95 % CIs. Data points *above* the constant difference *line* ($y = 0$) displayed divergence in cohort sizes, while data points *below* that *line* displayed convergence of cohort sizes. Data exclude mesocosms where cannibalism occurred. See Table 1 for regression results. **b** Effects of young-cohort density (low *solid lines*, high *dashed lines*) and intercohort time interval on mean growth rates of old cohorts (*black lines*) and young cohorts (*gray lines*). The response variable is mean mass gain in mesocosms where cannibalism did not occur, between days 36–94 of the experiment (i.e., period when cohorts overlapped, before first metamorphosis). At low densities, young and old cohorts grew at similar rates. At high densities, the growth rates of the old cohort were retarded more severely than those of the young cohort. *Error bars* are ±1 SE

and size at metamorphosis involved all the tubs in each treatment, including those in which cannibalism occurred. In the $\Delta t = 22$, high-density treatment combination, we observed cannibalism in three out of nine tubs. In the other six tubs, cannibalism did not happen, or there was a single cannibalistic event at the final days of the experiment (in one tub). To present the very different outcomes with and without cannibalism, we split this treatment combination to two means in the relevant figures.

Results

Initial size structure, characterized by size differences between cohorts, resulted from natural variation in larval sizes at birth, or from varying intercohort time intervals (Fig. 1a). The magnitude of these initial size differences had a marginally significant, weakly negative effect on size-difference development to day 94 ($p = 0.068$; Table 1), when the larvae had completed most of their growth and prior to first metamorphosis. Thus, size differences generally remained constant. Young-cohort densities had a significantly negative effect on intercohort size differences ($p = 0.007$; Table 1). Specifically, under low young-cohort densities, mean size differences remained constant over

Table 1 ANCOVA test for the effects of initial intercohort size differences and larval densities on the development of intercohort size difference by day 94 (before first metamorphosis), excluding tubs where cannibalism occurred

Source	SS	df	F ratio	p
Density	20,381.472	1	7.867	0.007
Initial difference	9031.016	1	3.484	0.068
Density × initial difference	1589.289	1	0.613	0.438
Error	119,225.94	46		

Table 2 Two-way ANOVA tests for the effects of intercohort time interval (Δt) and young-cohort density on larval fitness proxies

Response variable	Factor	df	F	p
Old cohort				
Larval mortality	Δt	1,31	1.56	0.221
	Density	1,31	28.95	<0.0005
	$\Delta t \times$ density	1,31	0.82	0.382
Size at metamorphosis	Δt	2,38	7.34	0.002
	Density	1,38	1.77	0.192
	$\Delta t \times$ density	2,38	4.46	0.018
Time to metamorphosis	Δt	2,38	1.82	0.177
	Density	1,38	1.58	0.216
	$\Delta t \times$ density	2,38	3.94	0.028
Young cohort				
Larval mortality	Δt	2,47	4.67	0.014
	Density	1,47	46.79	<0.0005
	$\Delta t \times$ density	2,47	1.06	0.353
Size at metamorphosis	Δt	2,39	3.06	0.059
	Density	1,39	13.13	0.0008
	$\Delta t \times$ density	2,39	0.52	0.598
Time to metamorphosis	Δt	2,40	43.51	<0.0005
	Density	1,40	2.84	0.100
	$\Delta t \times$ density	2,40	0.86	0.431

time [Fig. 1a; the 95 % CI of the low density regression line included the zero change line ($y = 0$)]. Under high young-cohort densities at $\Delta t = 22$, however, intercohort size differences reduced over time (Fig. 1a; the 95 % CI of the high density regression line excluded the zero change line). This was the result of more severe density-dependent retardation of growth rates in the old cohort, compared to the young cohort (Fig. 1b). Generally, there was a limited increase in size variation within cohorts over time, except for the few cannibalistic individuals who grew to exceptionally large sizes.

We recorded a total of 18 cannibalism events. Early-stage cannibalism (i.e., before day 94) was expressed rarely, only in three tubs. Over half (10) of the cannibalistic events occurred late in the season, after metamorphoses had begun (i.e., after day 94). Cannibalism was carried out by a few old-cohort individuals (a total of 9 larvae across 7 tubs), and occurred mostly in the $\Delta t = 22$, high-density treatment (4 out of 9 tubs). Some cannibalism also occurred in the $\Delta t = 9$, high-density treatment (2 out of 9 tubs), and in the $\Delta t = 9$, low-density treatment (1 out of 9 tubs). Cannibalism never occurred in the zero time interval treatments, nor was any member of the old cohorts ever cannibalized. Cannibals generally metamorphosed quickly after consuming their sympatric conspecifics.

Intercohort time intervals did not significantly reduce old-cohort mortality, but higher densities of the young cohorts significantly increased it ($p < 0.0005$; Table 2). Other than the successful metamorphosis primarily of old-cohort larvae that expressed cannibalism, the general mortality of the old cohort was almost entirely due to desiccation of the pools before the completion of metamorphosis (Fig. 2a). In contrast, mortality in the young cohorts increased significantly both with greater intercohort time intervals ($p = 0.014$; Table 2) and with higher densities ($p < 0.0005$; Table 2), the latter exerting a stronger effect. Mortality in the young cohorts was mostly the result of either desiccation prior to metamorphosis, or due to cannibalism (Fig. 2b). General survival patterns of the larval population, therefore, depended strongly on larval densities but not on intercohort time interval (Fig. 2c), such that larval recruitment to the adult population was negatively related to initial larval densities.R

Mean time to metamorphosis of the old cohort was not significantly affected by either of the main effects. However, the $\Delta t \times$ density interaction was significant ($p = 0.028$; Table 2). The more favorable treatment combinations ($\Delta t = 22$ days, and low densities at $\Delta t = 9$ days) resulted in shorter larval periods than the more stressful combinations ($\Delta t = 0$ and the high densities treatment at $\Delta t = 9$ days; Fig. 3a). Comparing the alternative outcomes of the $\Delta t = 22$, high-density treatment shows that without cannibalism, old-cohort survivors metamorphosed at
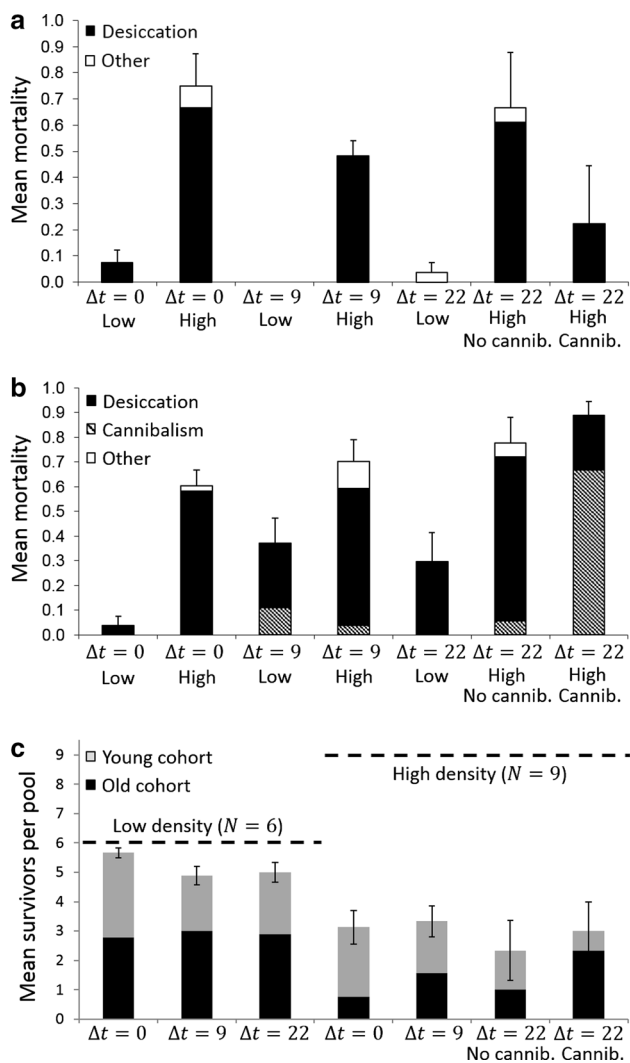
Fig. 2 Effects of treatment combinations of intercohort time interval ($\Delta t = 0, 9, 22$ days) and young-cohort densities (high/low) on larval mortality in **a** the old cohort, and **b** the young cohort. *Error bars* are ± 1 SE for total mortality. **c** Mean survival to metamorphosis (*stacked bars*), broken down by cohort (*black/gray shading*). *Horizontal dashed lines* indicate initial larval densities (of both cohorts) for low and high density treatments. *Error bars* are ±1 SE for total number of recruits (from both cohorts). The $\Delta t = 22$, high density treatment combination is split into tubs where cannibalism did not occur ($n = 6$) and where it occurred ($n = 3$). Note the change in order of treatment combinations in (**c**)

a similar age to those in the more stressful treatments. In contrast, with cannibalism, old cohorts metamorphosed at an early age. These results suggest that available resources were allocated preferentially to differentiation and metamorphosis rather than to growth. Size at metamorphosis of the old cohort generally increased with Δt ($p = 0.002$, log-transformed). Additionally, the $\Delta t \times$ density interaction was statistically significant ($p = 0.018$). Thus, size at metamorphosis followed a similar pattern as time to metamorphosis, where favorable treatment conditions generally
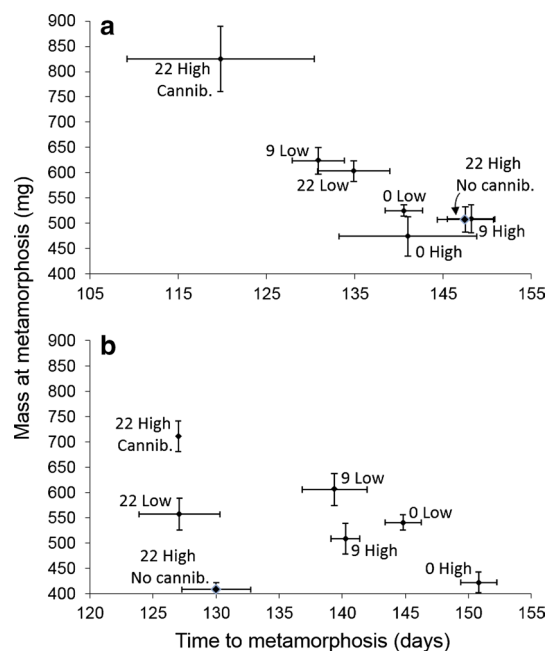

Fig. 3 Effects of treatment combinations of intercohort time interval ($\Delta t = 0, 9, 22$ days) and young-cohort densities (high and low) on mean time to (*horizontal axis*) and size at (*vertical axis*) metamorphosis in **a** old cohort larvae, and **b** young-cohort larvae. *Error bars* are ±1 SE. The $\Delta t = 22$, high density treatment combination is split into tubs where cannibalism did not occur ($n = 6$) and where it occurred ($n = 3$)

resulted in greater body sizes, including in the comparison between cannibalistic and non-cannibalistic old cohorts in the $\Delta t = 22$, high density treatment (Fig. 3a). The effect of intercohort interval on body size was the result of the initial time spent by the old cohorts growing at lower densities and experiencing low competition, and due to cannibalism.

Ages at metamorphosis of young cohort larvae were significantly lower with increasing Δt ($p < 0.0005$; Fig. 3b), as a result of the shorter time available for development. This suggests, as with the old-cohorts, that available resources were allocated by the larvae primarily to differentiation and metamorphosis. However, size at metamorphosis of young cohort larvae was significantly reduced only by larval densities ($p < 0.001$, rank transformed). However, young-cohort larvae that survived cannibalism in the $\Delta t = 22$, high-density treatment, achieved greater sizes at metamorphosis, probably as a result of substantial population thinning.

Discussion

Intercohort size differences in salamanders might be expected to increase over time, since strong interference of large individuals towards smaller ones has been

documented (Smith 1990; Reques and Tejedo 1996), including in this species (Eitam et al. 2005), and is readily observed in the field (Warburg et al. 1979; Degani 1993; Sadeh, personal observations). Yet, in this study, initial size differences that were generated by intercohort time intervals mostly remained constant over time at low young-cohort densities, regardless of their magnitude (Fig. 1). Furthermore, size differences generally reduced over time at high young-cohort densities, as a result of retarded old-cohort growth rates. Exceptions to this included all the pools where members of the old cohort cannibalized young-cohort victims and the body sizes of the cannibals subsequently diverged strongly from those of the rest of the population. Thus, the positive effect of interference on the development of intercohort size variation is fundamentally outweighed by opposing factors.

When individuals of all sizes exploit the same resource niche, increasing population density magnifies the importance of exploitative competition relative to interference, and may therefore limit the development of size variation (Huss et al. 2008b). That initial size differences in this study tended to diminish over time only at high young-cohort densities (in the absence of cannibalism), but not at low young-cohort densities, indicates that density-dependent competitive effects exerted by young cohorts on the older cohorts are stronger than those exerted by the young cohort on itself. This may be the result of three, but non-mutually exclusive, mechanisms: size-dependent growth rates, exploitative superiority of smaller larvae, or density-dependent reduction in aggressive interference by the old cohort. In the absence of any functional differences between size classes, the lower intrinsic growth rates of larger larvae compared to smaller ones, can lead to faster convergence of size differences with greater densities or with lower resource availabilities (Werner 1994). In addition, young larvae may have an exploitative advantage as a result of feeding preferentially or more efficiently on the smaller, earlier stages of prey crustaceans, thus reducing the availability of the larger prey stages that may be preferred by the older larvae. Finally, aggressive interference can be related positively to resource level when their availability is low (Grant et al. 2002) and therefore related negatively to larval density. However, while we did not measure the frequency of aggressive behavior, we often observed characteristic interference behaviors ('move-toward', 'lunge', and 'bite'; as defined in Walls and Jaeger 1987) between pairs of individuals across treatments. According to resource defense theory, the negative relationship between density and interference is the result of high per-encounter costs of aggressive behavior, relative to the benefit of monopolizing resources. However, interference in this species, as in many salamanders, involves cannibalistic attempts or at least the potential to escalate to cannibalism, therefore leading to

greater per-encounter benefits of aggressive behavior compared to non-cannibalistic forms of interference. Thus, we suggest that the decrease in the old cohort's size advantage at high densities is more likely a result of exploitative competition or its size-dependent effect on larval growth than due to reduced aggressiveness. However, low levels of cannibalism clearly enabled these factors to take effect.

Since cannibalism was rare, we could focus on the processes that operate in its background (i.e., exploitative competition and nonlethal interference) and that are typically masked in its presence. However, cannibalism is expressed frequently by larvae of this species, including in mesocosm studies similar to the current study (Sadeh et al. 2009; Sadeh 2012). The conditions in which cannibalism occurred reinforce the general notion that this behavior is promoted by sufficiently large size variation (Polis 1981; Anholt 1994; Claessen et al. 2000; Wissinger et al. 2010). Cannibalism can be prevalent in the field partly because intercohort time intervals can be even longer than 22 days, depending on rainfall patterns that determine larviposition by females (Sadeh and Blaustein, personal observations). With sufficiently large size differences, the role of the young cohort as prey is more pronounced, and the system may resemble one where the larger individuals have reached an ontogenetic diet shift to being cannibalistic (Claessen et al. 2000). In these conditions, higher young-cohort densities are expected to elevate the occurrence of cannibalism due to its functional response (Huss et al. 2010), and further exaggerate size variation. The notable differences in the frequencies of expression of cannibalism between studies of similar conditions highlight our limited understanding of the environmental factors that modulate this important behavior.

Across time interval treatments and cohorts, larval density had a strong effect on mortality, greatly increasing the proportion of larvae that failed to develop in time before the pools dried. Higher young-cohort density resulted in an increase in desiccation mortality of the older cohorts by a factor an order of magnitude greater than that of the young-cohort (Fig. 2a, b). Thus, in the absence of cannibalism, desiccation can lead to over-convergence of recruitment densities (i.e., greater recruitment from lower initial densities; Fig. 2c) due to strong mortality both in young and in old cohorts. This recruitment pattern may potentially result in adult population cycles (Hastings and Costantino 1991; Claessen et al. 2004). On the other hand, cannibalism tends to occur with large intercohort intervals and high young-cohort densities. When cannibalism occurs, mortality of the young cohort does not change, as cannibalism merely replaces desiccation. In contrast, the old cohort enjoys relieved mortality (see also Sadeh 2012). Cannibals benefit developmentally from increased conspecific prey densities, and are therefore less prone to death by habitat desiccation (see also Sadeh et al. 2009; Sadeh 2012),

in agreement with theory for organisms that experience time limitations on growth (Polis 1981; van den Bosch et al. 1988). This may lead to larger and more fecund recruits emerging from such pools. Cannibalism might also reduce the over-convergence of recruitment densities (e.g., Hopper et al. 1996), potentially attenuating population cycles. Future studies might advance the conservation of this endangered species by linking intercohort interactions and recruitment patterns with postmetamorph performance and adult population dynamics (Wissinger et al. 2010).

In conclusion, intra-population size variation is important in driving behavioral interactions and the resulting recruitment patterns from ephemeral larval habitats to the post-metamorph population. While the opportunity for cannibalism is the main advantage conferred to early larval cohorts when initial size variation is sufficiently high, and high young-cohort density increases the probability of cannibalism, old-cohort larvae that do not cannibalize are more vulnerable to density-dependent competition and mortality from desiccation. This suggests a key role of cannibalism in switching the direction of density dependence. Also, the balance of larval densities and cannibalism can alter the relative recruitment rates from different larval cohorts to the post-metamorph population.

References

Anholt BR (1994) Cannibalism and early instar survival in a larval damselfly. Oecologia 99:60–65

Bar-David S et al (2007) Long-distance movements by fire salamanders: integration of capture-recapture and genetic data and implications for conservation. Ecological Society of America Annual Meeting Abstracts

Blank L et al (2013) Genetic population structure of the endangered fire salamander (*Salamandra infraimmaculata*) at the southernmost extreme of its distribution. Anim Conserv 16:412–421

Blaustein L, Friedman J, Fahima T (1996) Larval *Salamandra* drive temporary pool community dynamics: evidence from an artificial pool experiment. Oikos 76:392–402

Claessen D, de Roos AM, Persson L (2000) Dwarfs and giants: cannibalism and competition in size-structured populations. Am Nat 155:219–237

Claessen D, de Roos AM, Persson L (2004) Population dynamic theory of size-dependent cannibalism. Proc R Soc Lond B 271:333–340

De Block M, Stoks R (2004) Cannibalism-mediated life history plasticity to combined time and food stress. Oikos 106:587–597

Degani G (1993) Cannibalism among *Salamandra salamandra* (L) larvae. Isr J Zool 39:125–129

Degani G, Goldenberg S, Warburg MR (1980) Cannibalistic phenomena in *Salamandra salamandra* larvae in certain water bodies and under experimental conditions. Hydrobiologia 75:123–128

Eitam A, Blaustein L (2002) Noninvasive individual identification of larval *Salamandra* using tailfin spot patterns. Amphib Reptil 23:215–219

Eitam A, Blaustein L, Mangel M (2005) Density and intercohort priority effects on larval *Salamandra salamandra* in temporary pools. Oecologia 146:36–42

Grant JWA, Girard IL, Breau C, Weir LK (2002) Influence of food abundance on competitive aggression in juvenile convict cichlids. Anim Behav 63:323–330

Hastings A, Costantino RF (1991) Oscillations in population numbers: age-dependent cannibalism. J Anim Ecol 60:471–482

Hjelm J, Persson L (2001) Size-dependent attack rate and handling capacity: inter-cohort competition in a zooplanktivorous fish. Oikos 95:520–532

Hopper KR, Crowley PH, Kielman D (1996) Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. Ecology 77:191–200

Huss M, Bystrom P, Persson L (2008a) Resource heterogeneity, diet shifts and intra-cohort competition: effects on size divergence in YOY fish. Oecologia 158:249–257

Huss M, Bystrom P, Strand A, Eriksson LO, Persson L (2008b) Influence of growth history on the accumulation of energy reserves and winter mortality in young fish. Can J Fish Aquat Sci 65:2149–2156

Huss M, van Kooten T, Persson L (2010) Intra-cohort cannibalism and size bimodality: a balance between hatching synchrony and resource feedbacks. Oikos 119:2000–2011

Kaspersson R, Höjesjö J, Pedersen S (2010) Effects of density on foraging success and aggression in age-structured groups of brown trout. Anim Behav 79:709–715

Loman J (2002) When crowded tadpoles (*Rana arvalis* and *R. temporaria*) fail to metamorphose and thus fail to escape drying ponds. Herpetol J 12:21–28

Persson L (1985) Asymmetrical competition: are larger animal competitively superior? Am Nat 126:261–266

Polis GA (1981) The evolution and dynamics of intraspecific predation. Annu Rev Ecol Syst 12:225–251

Polis GA (1988) Exploitation competition and the evolution of interference, cannibalism and intraguild predation in age/size-structured populations. In: Ebenman B, Persson L (eds) Size-structured populations: ecology and evolution. Springer, Berlin

Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509

Reques R, Tejedo M (1996) Intraspecific aggressive behaviour in fire salamander larvae (*Salamandra salamandra*): the effects of density and body size. Herpetol J 6:15–19

Sadeh A (2012) Kin-selective cannibalism and compensatory performance in larval salamander cohorts inhabiting temporary pools. Evol Ecol Res 14:113–123

Sadeh A, Mangel M, Blaustein L (2009) Context-dependent reproductive habitat selection: the interactive roles of structural complexity and cannibalistic conspecifics. Ecol Lett 12:1158–1164

Sadeh A, Truskanov N, Mangel M, Blaustein L (2011) Compensatory development and costs of plasticity: larval responses to desiccated conspecifics. PLoS ONE 6:e15602

Segev O, Blaustein L (2014) Influence of water velocity and predation risk on fire salamander (*Salamandra infraimmaculata*) larval drift among temporary pools in ephemeral streams. Freshw Sci 33:950–957

Segev O, Mangel M, Wolf N, Sadeh A, Kershenbaum A, Blaustein L (2011) Spatiotemporal reproductive strategies in the fire salamander: a model and empirical test. Behav Ecol 22:670–678

Smith CK (1990) Effects of variation in body size on intraspecific competition among larval salamanders. Ecology 71:1777–1788

Spencer M, Schwartz SS, Blaustein L (2002) Are there fine-scale spatial patterns in community similarity among temporary freshwater pools? Glob Ecol Biogeogr 11:71–78

Steinfartz S, Veith M, Tautz D (2000) Mitochondrial sequence analysis of *Salamandra* taxa suggests old splits of major lineages and postglacial recolonizations of Central Europe from distinct source populations of *Salamandra salamandra*. Mol Ecol 9:397–410

van den Bosch F, de Roos AM, Gabriel W (1988) Cannibalism as a life boat mechanism. J Math Biol 26:619–633

Walls SC, Jaeger RG (1987) Aggression and exploitation as mechanisms of competition in larval salamanders. Can J Zool 65:2938–2944

Warburg MR (1992) Breeding patterns in a fringe population of fire salamanders, *Salamandra salamandra*. Herpetol J 2:54–58

Warburg MR, Degani G, Warburg I (1979) Growth and population structure of *Salamandra salamandra* (L) larvae in different limnological conditions. Hydrobiologia 64:147–155

Werner EE (1994) Ontogenetic scaling of competitive relations: size-dependent effects and responses in two anuran larvae. Ecology 75:197–213

Wissinger SA, Whiteman HH, Denoel M, Mumford ML, Aubee CB (2010) Consumptive and nonconsumptive effects of cannibalism in fluctuating age-structured populations. Ecology 91:549–559

Ziemba RE, Collins JP (1999) Development of size structure in tiger salamanders: the role of intraspecific interference. Oecologia 120:524–529

Ziemba RE, Myers MT, Collins JP (2000) Foraging under the risk of cannibalism leads to divergence in body size among tiger salamander larvae. Oecologia 124:225–231