

Article

Similar Response of a Range Expanding Dragonfly to Low- and High-Elevation Predators

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Abstract: Recent range expansion of many species northward and upward in elevation suggests that the expanding species are able to cope with new biotic interactions in the leading edge. To test this hypothesis, we used a common garden experiment expanding the elevation range of an obligatorily univoltine dragonfly (*Sympetrum striolatum*) to investigate whether the growth, behavioral (food intake), and morphological (8th and 9th abdominal lateral spine) responses differed when confronted with dragonfly predators that dominate low-elevation (*Aeshma cyanea*) and high-elevation (*A. juncea*) lentic freshwater systems under two temperature treatments (20 °C and 24 °C). Growth rate and growth efficiency increased at higher temperature. Overall, low- and high-elevation predators induced a similar increase in growth rate and growth efficiency but a decrease in food intake at 24 °C. Lateral abdominal spines were longer only in low-elevation dragonflies at 18 °C. Our study suggests that range-expanding species may have been successful in colonizing new areas at higher elevations because they respond to dominant high-elevation predators in a similar way to the more familiar low-elevation predators.

Keywords: biotic responses; freshwater; Odonata; life history; chemical cues



Citation: Zebsa, R.; Mahdjoub, H.; Khelifa, R. Similar Response of a Range Expanding Dragonfly to Low- and High-Elevation Predators. *Diversity* **2022**, *14*, 302. <https://doi.org/10.3390/d14040302>

Academic Editors: M. Olalla Lorenzo-Carballa and Ricardo Koroiva

Received: 16 February 2022

Accepted: 12 April 2022

Published: 15 April 2022

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1. Introduction

To comprehend and predict future climate impacts on freshwater communities, there is growing interest in the biotic response of species to new colonizer species and its consequences on life history traits [1–5]. The ability to recognize and respond to different types of predators is a key trait that contributes to the successful establishment of new populations [6,7]. The response of growth rate to predatory stress has been widely investigated because of its intimate relationship with fitness [8]. Because the magnitude of biotic interactions (e.g., predation) can change with temperature, recent studies have focused on the thermal dynamics of predator-prey interaction to understand the outcome of range shift events that occur across geographic gradients such as latitude and elevation [9–11]. Both consumptive (visual cues) and non-consumptive (chemical cues) effects of predation can affect growth rate and induce changes in fitness-related traits [3,12,13]; however, studies on non-consumptive effects of cold-adapted (unfamiliar) predators on warm-adapted prey that gradually expand its geographic range to cooler areas are still lacking [4].

There are different physiological and behavioral mechanisms that determine growth rate, and understanding these mechanisms unravels some underlying plastic responses [5,14]. Usually, growth rate is a function of the amount of food ingested (food intake) and the amount of energy allocated to growth (growth efficiency) [15,16]. Thus, although a constant growth rate across an environmental gradient may be interpreted as an absence of the

adaptive response, it may hide dynamic plasticity in the behavioral and physiological components that contribute to the growth rate [17,18]. On one hand, an increased food intake likely increases individual activity and foraging behavior for prey acquisition, which often results in a higher mortality rate due to increased detectability by predators [7]. On the other hand, an accelerated growth efficiency leads to faster energy allocation and results in lower energy reserves and immune function [5,19]. Thus, it is important to understand whether behavioral and physiological components of the growth rate change in response to different types of predators and different temperatures to reveal the selective forces acting against the evolution of growth rate and predict the population dynamics of plasticity in new habitats after range expansion.

Apart from physiology and behavior, predators may induce plastic morphological responses such as defensive weaponry that reduces successful predation attempts [20,21]. As with growth efficiency, investment in defensive weaponry has survival costs and leads to a lower allocation of energy to other functional traits [22]. It has been shown that there is a negative relationship between behavioral and morphological defenses, so-called trait compensation [21,23]. Spending energy on defensive weaponry results in reduced vigilance while foraging. It is still not clear how species with time constraints respond to various types of predators, and which morphological, physiological, and/or behavioral mechanisms are prioritized.

While recent experimental studies have investigated the latitudinal patterns in predator-prey interactions [4,5], similar studies on the elevational gradient are still lacking. In the current study, we investigate the elevational range shift in Switzerland of *Sympetrum striolatum*, a widespread obligatorily univoltine species in North Africa, Europe, and Asia. To understand whether the species is able to cope with new biotic interactions at higher elevations, we assessed in a common garden experiment the response of growth rate, growth efficiency, food intake, and morphology (larval lateral spines) to temperature and different predation treatments. We exposed the species to two predators, a familiar (*Aeshna cyanea*: mainly at low elevations) dragonfly predator and an unfamiliar (*A. juncea*: mainly at high elevations) dragonfly predator. The low-high elevation dragonfly comparison reveals how the species would respond in a scenario of range shift to new habitats with a new predator, a phenomenon that has occurred repeatedly during the last decades [24,25]. Documenting the mechanisms controlling variation in growth rate across different treatments of predation and temperature is essential to understand the evolution of plasticity and predict future population dynamics in freshwater ecosystems [17].

2. Materials and Methods

2.1. Study Species and Distribution Data

Sympetrum striolatum is an obligatorily univoltine dragonfly that inhabits various types of wetlands, mostly stagnant freshwater, where it lays eggs from mid-summer to autumn and occupies an intermediate trophic level (as both predator and prey) in the freshwater food web. The species has shown a northward range expansion in the UK in recent decades [25], which makes it appropriate for the research question. In Switzerland, the species is historically considered a low-elevation species [26]. Long-term observations of adult *S. striolatum* carried out in Switzerland between 1990 and 2013 were obtained from CSCF (Centre Suisse de Cartographie de la Faune). The data included not only adult observations but also sex and reproductive states. To assess range shift across elevation, we included only records that showed a reproductive state such as copulation, oviposition, and emergence. The 95th percentile of the elevational distribution (leading edge) of *S. striolatum* and *A. cyanea*, and the 5th percentile (trailing edge) of the elevational distribution of *A. juncea* were calculated for each year to assess their historical changes during 1990–2013.

2.2. Study Site and Treatments

To investigate the effect of predation risk on the behaviour and physiology of dragonflies as well as the underlying proximate mechanisms, the response of larvae of *Sympetrum*

striolatum to two different predators was assessed in a common garden experiment in the laboratory at the University of Zurich, Switzerland. Eggs of *S. striolatum* were collected from two sites in Zurich, Switzerland (Irchel pond: 47.3977° N, 8.5448° E, 480 m elevation; Chatzensee pond: 47.4264° N, 8.4878° E, 440 m elevation). Both sites occurred within or near urban areas. We obtained the eggs from copulating females that were captured with a hand net in the middle of the day in early October 2015. The female abdomen was immersed in a vial with water, which led to the oviposition (about a few hundred eggs per female) [27]. Five different females from each site were sampled. Eggs were brought to the laboratory within two hours and put at room temperature (21 °C) and natural light conditions. Eggs of *S. striolatum* had a direct development and hatched within 2–3 weeks. After hatching, 20 larvae were placed in each of the six treatments (2 temperatures [18 °C, 24 °C] × 3 predation treatments [control, low-elevation, and high-elevation]) and raised individually in 180-mL plastic cups filled with dechlorinated tap water and floating on water tubs. Using polystyrene foam, the cups were able to remain floating on the surface of the water.

A randomized full factorial design using eggs from each of the two populations which were exposed to the combination of two predation treatments (low-elevation [*A. cyanea*] and high-elevation [*A. juncea*]) and two constant temperatures (20 and 24 °C). Temperatures were maintained by setting heaters at the bottom of water tubs. The low-elevation dragonfly was *Aeshna cyanea* and the high-elevation dragonfly was *A. juncea*, whose larvae were collected from Irchel forest (47.3893° N, 8.5611° E, 660 m) and Flumserberg (47.0661° N, 9.2546° E, 1904 m), respectively. Although the two species' elevational distribution overlap, the largest populations of each do not coexist at a similar elevation [26]. The two temperatures used in the experiment are far below the thermal critical maximum of *S. striolatum* [28].

Larvae under predation treatments received only chemical (no visual) cues from predators. The predator medium containing chemical cues was acquired by individually setting the predators (four large dragonfly larvae [size > 4 cm] in containers filled with dechlorinated tap water [12 × 12 cm filled to the height of 4 cm]). All predators were fed every day with a single *S. striolatum* larva (body length: 0.5–1 cm). We mixed together the chemical cues of four individuals of the same predator species, then 1 mL of the solution was provided daily to the prey. All *S. striolatum* larvae were fed once a day with *Artemia* sp. nauplii (~80–110 individuals in 5 mL).

2.3. Growth Efficiency and Food Intake

During 60 days after hatching, growth rates were quantified by measuring the head width of larvae every four days, taking pictures with a stereoscope, and estimating the distance between the edges of the eyes to the nearest 0.01 mm using ImageJ v1.52. To estimate the growth efficiency, a 4-day experiment as described by Stoks, Swillen and De Block [5] was used on 60-day-old larvae. This experiment consists of weighing larvae from different treatments to the nearest 0.01 mg using an electronic balance at the start and the end of the 4-day period. Then growth rate was measured as $[\log(\text{final mass}) - \log(\text{initial mass})] / 4$ days, which accounts for differences in mass at the start of the experiment [18]. Given the widespread distribution of *Daphnia* in freshwater ecosystems worldwide, and its importance as prey to dragonflies [29], we provided *S. striolatum* larvae with 20 individual *Daphnia* of similar size each day. The number of *Daphnia* eaten per day was counted and replaced. The number of eaten daphnia was converted to total dry mass ingested using an equation [dry mass = a wet mass + b] established through weighing (to the nearest µg using an electronic balance) *Daphnia* before and after drought-treatment in the oven at 60 °C during 48 h. Dry mass of larvae was also estimated in the same way to obtain a conversion factor (dry mass = 0.114 × wet mass + 0.478).

2.4. Morphological Defense

Predation avoidance in freshwater prey might involve morphological modifications that reduce the probability of being eaten [1,20,21]. To test whether there is variability in the morphological response to different predator types, the 8th and 9th lateral abdominal spines of larvae were measured at the end of the experiments, 65 days after hatching. The size of lateral abdominal spines shows plasticity when exposed to predators [21]. The length of the spines was corrected for the larval size by dividing it by the head width of larvae; a widely used measure of body size which describes the developmental stage of larvae [30].

2.5. Statistical Analyses

All statistical analyses were carried out using R 3.5.1 [31]. We calculated the leading and trailing edge of the distribution of all three species using 95th and 5th percentile of the elevation of the occurrence data, respectively. Then, elevational range shift was assessed using simple linear regressions including our estimate of the elevational distribution edge (leading or trailing) as a response variable and years as an explanatory variable. To determine differences in growth rate among treatments, linear mixed-effects (LME) model including head width as a response variable and time (days), predation and temperature as explanatory variables, and individual identifier as a random effect, was carried out using *lme4* package [32]. We used the *lstrends* function from *lsmeans* package [33] on our LME model to calculate for each treatment average growth rate with 95% confidence intervals. Since we had a single measure per individual (no repeated measures), we used a linear model to determine the difference in growth efficiency, food intake and lateral spine length between temperature and predation treatments.

3. Results

3.1. Elevational Range Shift

The 95th margin of the elevational distribution (leading edge) shifted by 4.6 m/year (Figure 1; linear model: slope = 4.66 m/yr, $R^2 = 0.21$, $p = 0.02$). The trailing edge (5th percentile) of the high-elevation predator *A. juncea* did not show a significant shift (slope = -2.63 m/yr, $R^2 = 0.03$, $p = 0.40$), nor the leading edge of the low-elevation predator *A. cyanea* (slope = -12.2 m/yr, $R^2 = 0.14$, $p = 0.06$) during the same period.

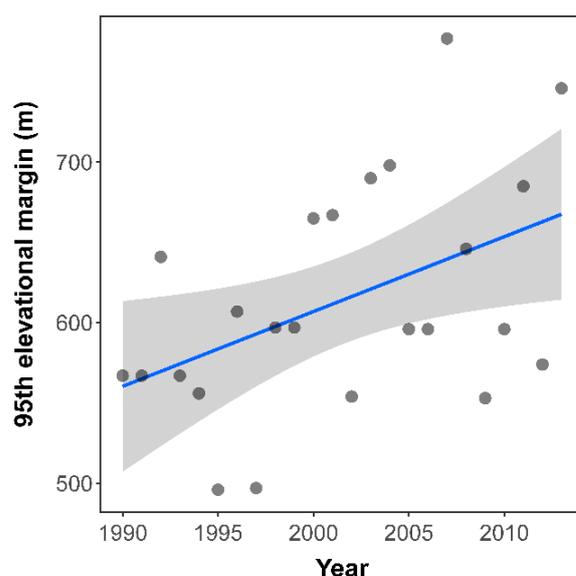


Figure 1. Historical changes of the leading elevational edge (95th percentile) of *Sympetrum striolatum* in Switzerland between 1990 and 2013. The linear regression was positively significant ($R^2 = 0.21$, $p = 0.02$), suggesting a historical shift towards higher elevations.

3.2. Larval Growth

Larvae grew faster in water at 24 °C than at 18 °C (LME: $p = 0.0001$; Table S1). Growth rate was significantly different among predation treatments (LME: $p = 0.002$; Table S1), revealing a faster growth in predation treatment compared to the control treatment (Figure 2). The significant interaction between time and temperature and the non-significant three-way interaction between time, temperature, and predation indicate that larvae responded similarly to the different predators at both temperatures ($p > 0.05$; Table S1).

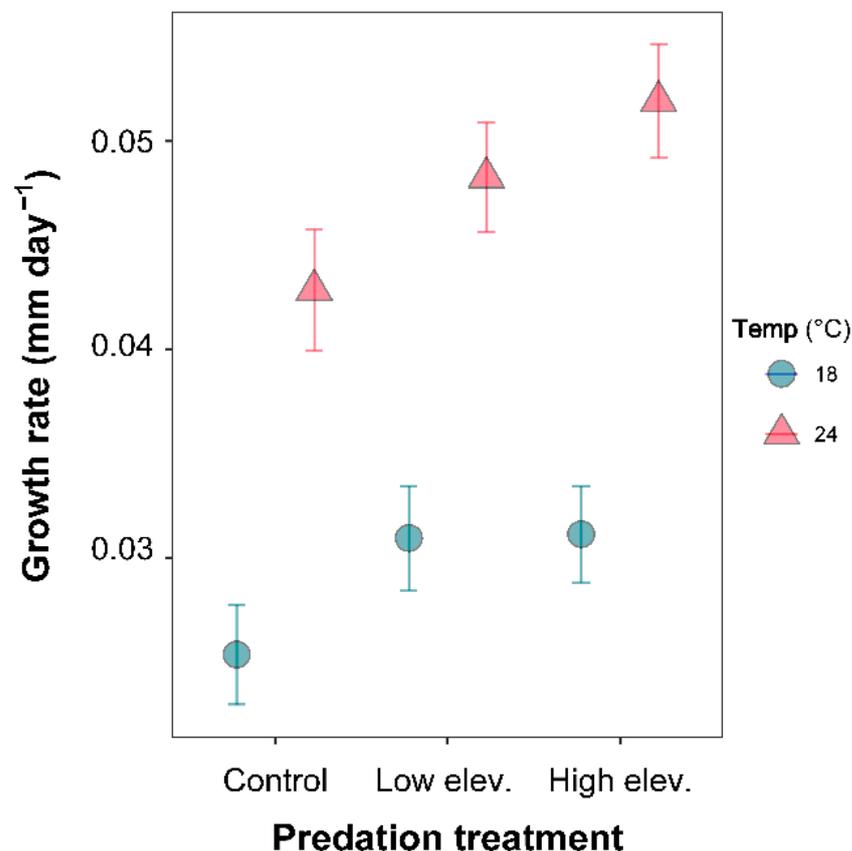


Figure 2. Growth rate of *Sympetrum striolatum* larvae in the combination of two temperature and three predator treatments. Error bars are 95% confidence intervals.

Growth efficiency was significantly different between temperature (LME: $p = 0.0002$) and predator treatments (LME: $p < 0.002$) (Figure 3). Growth efficiency was 81.6% greater at higher temperature than at lower temperature. Larvae in predation treatments showed a higher growth efficiency than in the control treatment, but there was no significant difference between low and high-elevation predator (Figure 3). There was a small significant interaction between temperature and predation treatment (Table S2).

3.3. Behavioral Response

There was a significant interaction between temperature and predation (Figure 4, Table S3). At 18 °C, larvae showed a lower food intake in high-elevation predator treatment ($p = 0.002$). At 24 °C, larval food intake was lower in both low- and high-elevation predator treatment than in the control, although marginal for the high-elevation predator (Table S3, $p = 0.01$; $p = 0.07$, respectively).

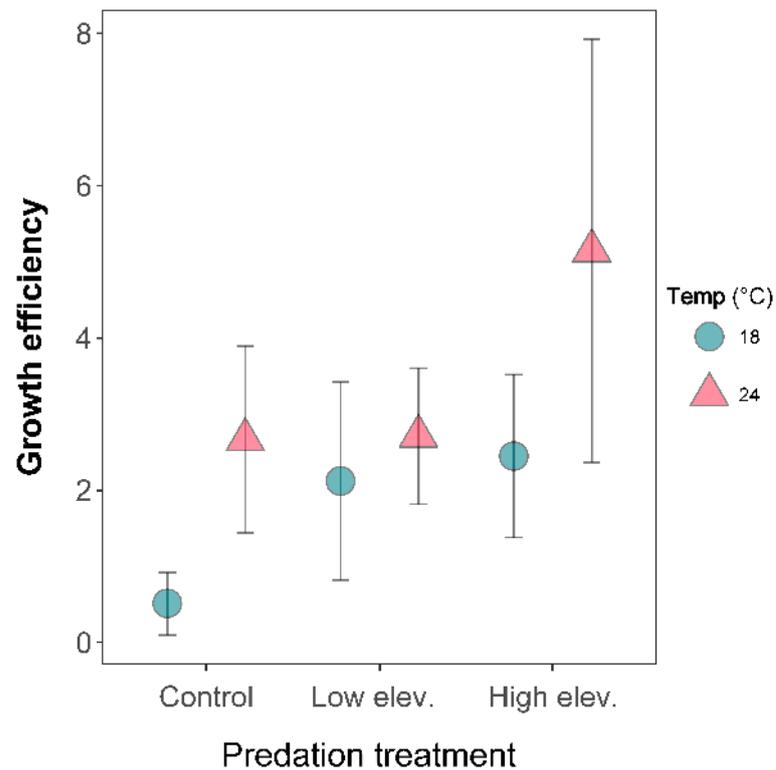


Figure 3. Growth efficiency of *Sympetrum striolatum* larvae in the combination of two temperature and three predator treatments. Error bars are 95% confidence intervals.

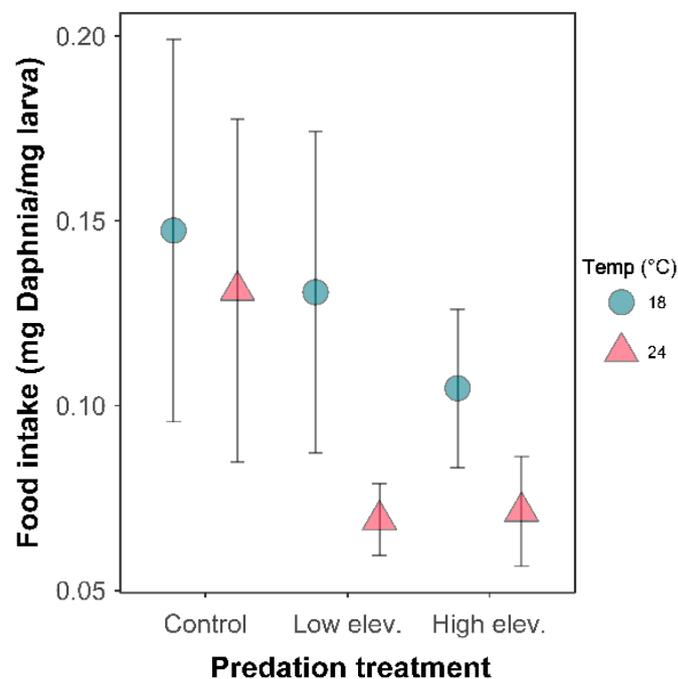


Figure 4. Food intake (corrected for body mass) of *Sympetrum striolatum* larvae in the combination of two temperature and three predator treatments. Error bars are 95% confidence intervals.

3.4. Morphological Response

The length of the 8th lateral spine was longer in the low-elevation dragonfly treatment ($p = 0.01$; Table S4a, Figure 5a), but neither temperature nor the interaction of temperature with predation showed a significant effect (Table S4a). The length of the 8th lateral spine

was 32% longer in the low-elevation predator treatment than in the control (Figure 5a, Table S4a). Similar to the 8th lateral spine, there was no significant effect of temperature on the length of the 9th lateral spine (Table S4b, $p = 0.64$). However, larvae in the low-elevation dragonfly treatment under 18 °C had significantly longer 9th spines than the other treatments ($p = 0.001$; Table S4b, Figure 5b). The average length of the 9th spine in the low-elevation predator treatment was 33% longer than that of the control.

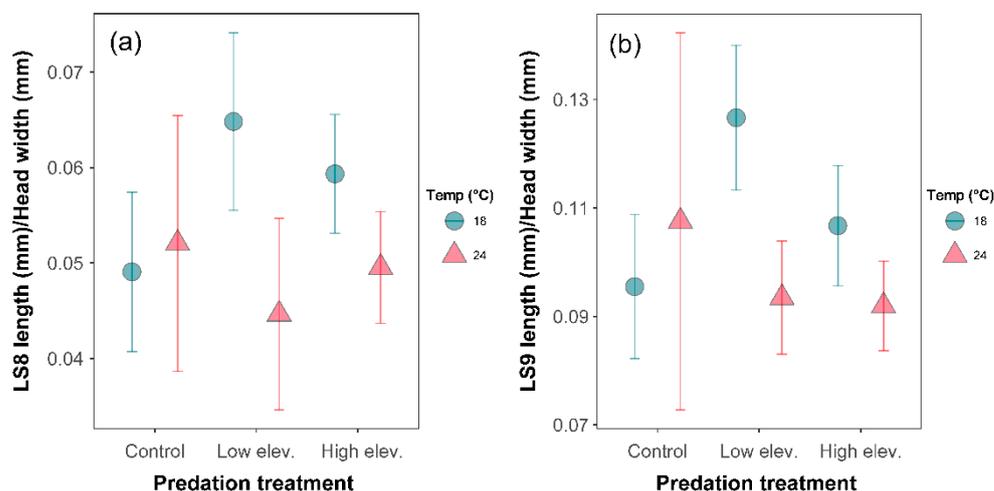


Figure 5. Length of the 8th (a) and 9th (b) lateral spine of *Sympetrum striolatum* larvae in the combination of two temperature and three predator treatments. Error bars are 95% confidence intervals.

4. Discussion

In this study, we showed that the low-elevation obligatorily univoltine *S. striolatum* expanded its range by 4.6 m/yr across elevation during 1990–2013, which suggests that the species was able to adapt to the new biotic environment. The common garden experiments assessing the non-consumptive response of growth (rate and efficiency), behavior (food intake), and morphology (abdominal spine) of *S. striolatum* to different predators including low- (familiar) and high-elevation (non-familiar) dragonflies showed that overall dragonfly larvae responded similarly in growth and food intake to both predators, but they responded distinctly in morphology to the familiar dragonfly predator.

4.1. Range Shift

Sympetrum striolatum has shown an elevational range shift of 4.6 m/year between 1990 and 2013. The same species has been reported to expand its northern range limit in the UK by 346 km between 1960 and 1995, which is equivalent to a rate of 8.6 km/year [25]. Given that this species is still flourishing at low elevations and in the southern range limit, it can be inferred that the range has expanded both in latitude and elevations. Discrepancies between latitudinal and elevational range shift are probably due to the steeper cline in environmental conditions across elevation, which restricts the speed at which new populations are established at higher elevations. However, the successful establishment of higher elevation populations is probably due to recent climate warming in the Swiss Alps, but it also suggests that the species was able to cope with new biotic conditions. Furthermore, the absence of elevational shift of the trailing distribution edge of *A. juncea* suggests that the encounter probability between *S. striolatum* and *A. juncea* has increased. We suggest that the overlap will increase even further in the following years.

4.2. Temperature Effects

Temperature had various effects on growth, food intake, and length of lateral spines of larvae. Higher temperatures led to an increased growth rate and growth efficiency. In many taxa, growth rate is expected to increase with temperature when temperatures are below the thermal optimum [34], which is typically higher than 24 °C in temperate Libellulidae [35].

However, unlike studies on odonates [5,36] and butterflies [37] which found that the increase in growth rate was associated with an increase in food intake, our study showed that it was associated with an increase in growth efficiency [16]. Thus, it is likely that this is an adaptive mechanism that allows obligatorily univoltine species such as *S. striolatum* to respond to an increase in temperature by increasing growth efficiency despite lowering food intake. Such a strong physiological response probably has considerable fitness trade-offs for adults [38]. In a climate warming scenario, temperature-induced changes in physiology and behavior might have a major impact on predator-prey interaction and community structure [4,39,40]. For example, an increase of 4 °C (difference in temperature treatments in this study) causes an increase in growth rate and a decrease in food intake which may lead to an earlier emergence (shorter exposure of prey to predators) and a decline in predation rates (less prey eaten during the short exposure time). These effects may have direct [41] and indirect consequences [42] on the freshwater food web. Interestingly, a positive response in anti-predatory morphological defenses was observed only at low temperatures where food intake was higher, suggesting that at higher temperature larvae invested in growth rather than anti-predatory weaponry.

4.3. Predation Effects

The analysis of growth rate showed a significant difference among predator treatments. Unlike the commonly reported pattern of growth reduction under predation treatments [17,43], we found a predatory-induced acceleration of growth which was also reported in odonates [5,44–46] and other vertebrates [47,48]. One explanation of the increased growth rate under predation is the ‘escape theory’ which is predicted by some optimal models when non-predatory costs of growth exist [49,50]. This theory is further supported by the fact that many *Sympetrum* species are obligatorily univoltine [51], and thus environmental limitations such as predation or time constraints result in a fastening of growth rates [5,52]. This finding highlights the fact that the recent range shift of many large species of odonates, invertebrates, and vertebrates might alter the life history of many prey taxa of freshwater ecosystems, which might result in major evolutionary and ecological changes.

There was a lower food intake under dragonfly predation (both low- and high-elevation) than in the control, which suggests that larvae detected the predator through chemical cues and subsequently lowered their food intake probably to avoid being detected and eaten [2]. A similar decline in food intake under dragonfly predation was detected in damselflies [5,17] and dragonflies [53]. Furthermore, there was a higher growth efficiency under dragonfly treatment than in the control treatment, which means that larvae grew fast with respect to the amount of food consumed. A similar increase in growth efficiency has been observed in damselflies in the presence of predation [5]. The lower food intake and higher growth efficiency for a species adapted to time constraints could be theoretically explained by optimality models [50]. Food intake involves at least the movement of mouthpieces (mentum), which makes prey larvae detectable by large dragonfly predators. Thus, decreasing food intake is a common anti-predatory behavioral mechanism that individuals adopt to increase their survival probability [54]. High growth efficiency is a physiological anti-predatory response that allows larvae to minimize their exposure to predation and reach the adult stage as early as possible [55]. This hypothesis is supported by previous studies on many taxa carried out in freshwater ecosystems on odonates [45,46], frogs [48], and fish [3,47]. The costs of growth acceleration have been documented and could involve a weakening of the immune system and reduction in energy reserves [15], and could even carry over until the adult stage where individuals encounter shorter longevity and reproductive success [56].

Morphological responses to predators have been well documented in odonates, but mostly against fish [20,21,57]. Interestingly, our study showed a morphological response of the lateral abdominal spines when exposed to chemical cues of dragonfly predators. Studies have shown that fish reject larval dragonflies which have long abdominal spines,

thus allowing dragonflies to increase their survival probabilities [20]. It is unclear how longer spines benefit larvae from dragonfly predation. One likely hypothesis is that longer spines might be a by-product of physiological responses rather than an adaptive response to dragonfly predation [47]. In fact, higher growth efficiency might result in morphological changes that might include variation in the length or morphology of abdominal structures such as lateral spines. However, this hypothesis does not explain the observed longer lateral spines in low-elevation dragonfly treatment but not in high-elevation dragonfly treatment. This intriguing response to the more familiar predator warrants further investigations of the role of abdominal lateral spines against dragonfly predation.

While larvae used to estimate physiological and behavioral parameters had similar ages, there might be a difference in larval instars among individuals that might influence the response of larvae. Nevertheless, the observed physiological and behavioral responses were similar to other studies [5,45,48]. Since antipredator response can be costly in invertebrates in general [58], one would expect that selection should favor accuracy in detecting the predators that induce mortality or damage [59]. The fact that low- and high-elevation predators (*A. cyanea* and *A. juncea*) are closely related species with potentially similar diet could explain the similar behavioral and physiological response of *S. striolatum* larvae. Studies have linked the composition of chemical signals (kairomones) and predator diet [60–62]. The ability to detect a non-familiar predator is a dispersal asset for species, allowing larvae to develop, persist, and successfully establish a viable population in new habitats. For instance, many libellulids such as *S. striolatum* are invaders of ponds and lakes of northern and high-elevation areas [63], causing changes in species composition and probably competing with rare specialist species [35,64]. It could be that their success in invading new territories is due to their ability to respond similarly to new predators as their familiar predator. However, whether populations of *S. striolatum* at low elevations living in different types of landscapes (e.g., natural, suburban, or urban) respond similarly to different predators remains to be investigated. Our results suggest that species that successfully expanded their range to higher elevation habitats might be preadapted to the new biotic interactions. Future studies should investigate the implication of odonate range expansion on the dynamics of freshwater and terrestrial foodweb [65].

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14040302/s1>, Table S1: Summary results of the linear mixed-effects model regressing head width of *Sympetrum striolatum* against time, temperature and predation treatments. Table S2: Summary results of the linear mixed-effects model regressing growth efficiency of *Sympetrum striolatum* against temperature and predation treatments. Table S3: Summary results of the linear mixed-effects model regressing food intake of *Sympetrum striolatum* against temperature and predation treatments. Table S4: Summary results of the linear mixed-effects model regressing the length of the 8th (a) and 9th (b) lateral spine corrected for body size of *Sympetrum striolatum* against temperature and predation treatments.

Author Contributions: Conceptualization, R.K.; methodology, R.K., R.Z. and H.M.; software, R.K., R.Z. and H.M.; validation, R.K.; formal analysis, R.Z.; investigation, R.K., R.Z. and H.M.; data curation, H.M.; writing—original draft preparation, R.K. and R.Z.; writing—review and editing, R.K., R.Z. and H.M.; visualization, H.M.; supervision, R.K.; funding acquisition, R.K. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Swiss National Science Foundation, grant number P2ZHP2_175028. The APC was funded by Swiss National Science Foundation.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Acknowledgments: We would like to thank the Centre suisse de cartographie de la faune and Christian Monnerat for providing the Swiss atlas data of odonates.

Conflicts of Interest: The authors declare no conflict of interest.

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