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Development of *Sympetrum striolatum* and *S. vulgatum* (Odonata: Libellulidae) in brackish water

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This article is dedicated to Reinhard Jödicke, the former editor of the International Journal of Odonatology, to his 75th anniversary. Reinhard, you did a great job!

Abstract. *Sympetrum striolatum* (Charpentier, 1840) and *S. vulgatum* (Linnaeus, 1758) are two closely related Libellulidae that are widespread and common in Central Europe. The idea for this research originates from normally using saltwater shrimps for rearing young larvae, the observations of *Sympetrum* species laying eggs in seawater and the suggested ability of *S. striolatum* to colonize brackish water habitats. This topic will also be of rising relevance for dragonfly populations as in the future due to climatic changes or anthropogenic activity the salinization of freshwaters will likely increase. The experiments presented in this study served to find out whether eggs and larvae of both species can develop in brackish water. For this purpose, eggs of both species were kept at four different salinities from 0.5–1.5% and the development duration, hatching curves and growth rates as well as mortality were recorded and compared to respective data from an earlier experiment conducted in tap water. It was possible to investigate whether embryonic development, the hatching behaviour and larval growth are disturbed by different salinity levels compared to rearing in freshwater. We found for both species that the eggs can develop at different salt concentrations up to 1.5% and the larvae survive and grow in the brackish water. Especially for *S. striolatum* a slightly increased salinity even seems to be advantageous compared to rearing in tap water shown by high hatching and survival rates. The results of this study add some knowledge about the influencing effects of salt on both species. It seems that low salt concentrations seem to be well tolerated by both species or become even beneficial for *S. striolatum*. Furthermore, the results provide methodological aspects about the rearing of young dragonfly larvae.

Key words. Anisoptera, egg development, larval growth, salt, survival

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Data Availability Statement:
All relevant data are within the paper.

Introduction

Dragonflies are usually perceived as semiaquatic organisms, which develop in freshwaters (Corbet, 1999; Suhling et al., 2015). Already Osburn (1906) suggested that the metabolism of dragonflies is disturbed above a certain salt concentration. Corbet (1999) concluded that larvae of most Odonata are hyperosmotic regulators, i.e., they are incapable of hypoosmotic regulation as salinity increases beyond a level at which the haemolymph becomes isotonic with the external medium. Osmoregulation has only been investigated in a few odonate species (Komnick, 1978, 1982). There are species that seem to tolerate (Catling, 2009) or even be associated with water of higher salt content: the best-known example may be *Erythrodiplax berenice* (Drury, 1770). This species is associated with marine habitats, breeding for instance in mangrove flats and salt marshes in North, Central and parts of South America (Dunson, 1980; Wilson, 2008). The habitats of *E. berenice* have salinities of up to 36–48 ppt, which is above the average level of seawater (3.5%, 35 ppt) (Dunson, 1980). *Macrodiplax cora* (Brauer, 1867) seems to occur mainly in coastal habitats of the Indian and Pacific Ocean (e.g. Lambret et al., 2017). Also, the European *Lestes macrostigma* (Eversmann, 1836) is a typical brackish water species found at salinity of up to 28.5 g/l (approx. 2.8%) during the main emergence period (Lambret et al., 2021, 2023; Lambret, com. pers.). In general, species from ephemeral waters in arid areas may be able to cope with higher salt concentrations which may rise while the water is evaporating, e.g. up to 42 mS/cm in Namib desert ponds (Suhling et al., 2003), although the high conductivity in those ponds may be due to other salts than Sodium-Chloride. Considering such observations there may be a wider range of salinity concentrations Odonata larvae may adapt to, however the physiological processes are functioning in these environments.

However, little is known about these processes even though an important environmental problem is the increasing salinization of freshwaters (Hintz & Relyea, 2019). There are various causes of freshwater salinization such as naturally higher salinization due to sea spray (Fernández-Martínez et al., 2019), climate change, anthropogenic modification of freshwater, and freshwater cycles (Herbert et al., 2015), or the use of salt for road safety (Schuler et al., 2017). Therefore, the impact of salt on Odonata becomes an interesting research topic because increased salinity may have an impact on dragonfly populations, as salt can potentially affect the development of eggs and larvae.

Some observations suggest that *Sympetrum* larvae can cope with higher salinity to some extent. *Sympetrum* species such as the Central Asian *S. tibiale* (Ris, 1897) prefers brackish water (Dumont et al., 2018) or *S. costiferum* (Hagen, 1861), *S. danae* (Sulzer, 1776), *S. internum* (Montgomery, 1943), and *S. obtrusum* (Hagen, 1867) from the Canadian province of Quebec which emerged from brackish ponds (Catling, 2009). There are observations of *S. striolatum* among other *Sympetrum* species ovipositing in salt water of the Mediterranean and North Seas (Utzeri et al., 1991; Suhling, pers. observ.). Are these eggs able to develop at all and if they do, how does the salty water affect egg and larval development? Also, Wildermuth & Martens (2019) emphasize that *S. striolatum* colonises brackish water habitats. But emergence from brackish or saline water habitats has not been described yet.

While we did a study on the development of *S. vulgatum* and *S. striolatum* (Hogreve & Suhling, 2022), we became interested how development of both species were affected by increased salinity. In this study we reared eggs and larvae of *S. striolatum* and *S. vulgatum* at four different salt concentrations, viz. 0.5, 0.7, 1.0 and 1.5% NaCl, in order to investigate whether the eggs can develop at all in salty water, how egg development and larval growth are affected. We compared the duration of egg development, hatching rates, larval mortality, and growths rates with the same parameters measured in experiments conducted in tap water (Hogreve & Suhling, 2022). This was mainly because we wanted to know, whether eggs can develop in salty environments and because we normally feed the young instar larvae with brine shrimp naupliae (*Artemia* sp.), which is often used as food in experiments with early instar larvae (Everling & Johansson, 2022; Frances et al., 2017; Jinguji et al., 2018; Suhling et al., 2015). This method will eventually affect the salinity conditions at least in small rearing containers especially if there are no regular water changes or the food has not been rinsed and might therefore influence the growth rates and behaviour of dragonfly larvae. Additionally, the *Artemia* sp. have a higher salt content, which the dragonfly larvae will consume when feeding on them.

Methods

The egg development and hatching behaviour and growth rates of *S. striolatum* and *S. vulgatum* were monitored at four different salt concentrations. For a comparison with freshwater conditions we used the mean values from data gained in another experiment (Hogreve & Suhling, 2022), which, however, was conducted under the same general condition described below. Tap water was used. The only difference was that in that experiment higher numbers of egg clutches were used for both species and that we calculated means ± standard deviation for all measured parameters based on the numbers of egg clutches (S. *striolatum* ten clutches, *S. vulgatum* eleven clutches).

For this experiment we collected eggs of two pairs of *S. striolatum* and two pairs of *S. vulgatum* by catching copulating or ovipositing tandems. All four clutches were collected in Braunschweig (52.2710° N, 10.5644° E) on the 11th September, 2020. For collecting the eggs a female's abdomen was dipped into a tube filled with water (Robert, 1959). The eggs were directly transferred to the laboratory, the clutches split and the eggs counted. The clutches of both females per species were mixed for the experiment. We assumed that the vast majority of eggs were fertilized because we observed colour change from pale to brown. All experiments were carried out under the same general laboratory conditions. Illumination was by LED daylight lamps (1600 lux) for 14 hours daily and the lab temperature varied between 18–22°C.

Rearing of eggs

We refer to brackish water as saltwater with less than 3% salt content. For classification: distilled water has barely any salt and a conductivity of approx. 0.2 µS/cm

Table 1. Effects of the salt concentration treatment on the development of *Sympetrum striolatum* and *S. vulgatum.* We recorded five parameters: the minimum duration of development until the first hatching occurred, the rate hatching from the eggs (i.e., survival rate), the duration of hatching until all surviving larvae had hatched, and calculated the time until 50% and 90% of the surviving larvae had hatched. Results of contingency table tests between the two species are shown.

	Treatment Salt [%]	No. of eggs	Hatching rate [%]	Min. duration development [d]	Hatching duration [d]	Q_{50} [d]	Q_{90} [d]
S. striolatum	Tap water	1873	64.7±19.0	11.4±0.7	59.5±50.5	1.2±1.2	7.8±8.1
	0.5	681	93.7	10	35	3	13
	0.7	741	97.2	11	44	7	22
	1.0	431	71.5	12	60	11	29
	1.5	339	28.3	17	28	10	22
S. vulgatum	Tap water	2829	62.7±14.6	26.5±14.7	150.9±21.5	51.0±15.6	90.4±16.8
	0.5	517	67.7	11	182	105	129
	0.7	467	47.5	11	133	98	116
	1.0	460	57.6	19	145	90	117
	1.5	276	44.9	17	147	78	103
		χ^2 =	17.795	4.169	18.753	9.892	12.102
		p =	0.001	0.384	<0.001	0.042	0.017

and marine sea water approx. 3.5%, i.e. 35 grams salt per litre and a conductivity of approx. 56 mS/cm. We reared eggs and larvae at salt concentrations of 0.5%, 0.7%, 1%, and 1.5%. For generating these concentrations, we mixed tap water, which was dechlorinated by filling it into buckets some days prior to the experiments, with respective amounts of marine salt. As a control, the conductivities of each concentration were measured before each usage. The respective conductivities were 0.3 mS/cm for tap water, 6.8–7 mS/cm for 0.5%, 9.5–10 mS/cm for 0.7%, 13–14 mS/cm for 1%, and 19–21 mS/cm for 1.5% salt. The water was exchanged weekly to prevent increase in salt concentration due to evaporation.

So, the experimental setup held eight containers: two species at four salt concentrations. They were monitored daily. Freshly hatched larvae were counted and removed from their container. By this an exact time series of the hatching for each treatment was recorded. With these data the development time of the clutch until first hatching and the total hatching duration, the hatching rates in percent of the total number of eggs per treatment was calculated and the hatching curves over time were plotted. To characterize and compare the shape of the hatching curves as patterns, the quantiles of 50% (Q_{50}) and 90% (Q_{90}) of the larval hatch were determined from the cumulative function (see Hogreve & Suhling, 2022). Correlation analyses and χ^2-tests comparing the two species were carried out for the egg development parameters and the salinity. Also, we fitted response curves with O'Neill functions.

Rearing of larvae

We aimed also to compare larval growth rates of both species at each concentration. For that it was required that we used larvae hatched under most comparable conditions. One of the conditions was that we wanted to raise larvae of similar age (i.e. hatched with not more than a week difference). For investigating the larval growth 40 larvae of *S. striolatum* at each salt level were reared. Since the hatching of *S. vulgatum* was much less synchronised that the hatching of *S. striolatum* (Hogreve & Suhling, 2022) the resulting numbers of *S. vulgatum* were low. We had 10 larvae at 0.5% salt, 12 larvae at 0.7%, four larvae at 1%, and two larvae at 1.5%. Consequently, the data for this species have to be treated with care. The larvae were reared at room temperature at their salty water concentrations and fed daily with naupliae of *Artemia* sp. Therefore, more food was available than consumed by the larvae. Small plastic boxes measuring 7.5 × 5.5 × 2.5 cm (L×W×H) filled with approximately 80 ml water were used for rearing, one container per species and salt concentration, i.e., larvae grew under conditions of competition for food with con-specifics. The larvae were counted and head widths of all surviving larvae were reared and measured weekly for three months. Linear regression was fitted to get the mean growth rates over time and the model performance of the fit was described by the coefficient of determination R^2. Correlation analysis between salinity and growth rate was tested.

Results

Egg development

The hatching rate differed between the two species (Table 1), with *S. striolatum* having higher rates at all salt concentrations, except 1.5%. In *S. striolatum* the hatching was highest at 0.5% and 0.7% salt and even at 1% salt the hatching was higher than the average in tap water. Only at 1.5% salt there was a clear drop in survival. The relation between salt content and hatching rate could be fitted with an O'Neill function (Fig. 1), i.e., resembling an optimum curve with intermediate salt content being beneficial. In *S. vulgatum* there was not such a clear relation between salt content and hatching rate but with survival still higher at 0.5% salt than in the tap water (Fig. 1). The minimal egg development duration (Table 1) for *S. striolatum* was not strongly affected by low salt contents as the values were not differing strongly from tap water treatment (0.5–1%) and slightly raised at high salinity (1.5%). *Sympetrum vulgatum* had high variations in tap water and developed faster in salty water than in tap water at low salinity levels (Table 1). In comparison to the lower concentrations the two higher salinity levels of 1% and 1.5% led to a delay in the minimal egg development duration.

Hatching pattern

The hatching duration differed between the two species with *S. striolatum* hatching faster (Table 1). The hatching duration of *S. striolatum* showed higher variation compared to the synchronous behaviour of the clutches in tap water. With increasing salinity, the hatching duration increased, then with 1.5% it dropped again. This means that not only the hatching rate decreased with high salinity, but also the hatching process was shortened. With *S. vulgatum*, low salinity led to a delayed hatching pattern, otherwise values of the hatching duration remained quite constant. The larval hatching of *S. striolatum* described by Q_{50} and Q_{90} took longer with rising salinity level (Table 1). *Sympetrum striolatum* showed a significant correlation between salt content and Q_{50}. Salt led to a change in the shape of the hatching curve characterized by the Q_{50} and Q_{90} by having a delaying effect (Table 1). The Q_{90} shows a less clear pattern for *S. striolatum*. With salt there is an increase, the duration until hatching of 90% of the larvae was almost doubled and then decreased again. Interestingly, the Q_{50} and Q_{90}-values of *S. vulgatum* were higher in low salinity and decreased with higher salt concentrations. But overall the salt had a delaying effect on the hatching process of *S. vulgatum* as the lowest Q_{50} and Q_{90} were measured in the tap water treatments (Table 1).

Larval growth

Contrary to the expectation the growth rates of both species were not strongly affected negatively by salin-

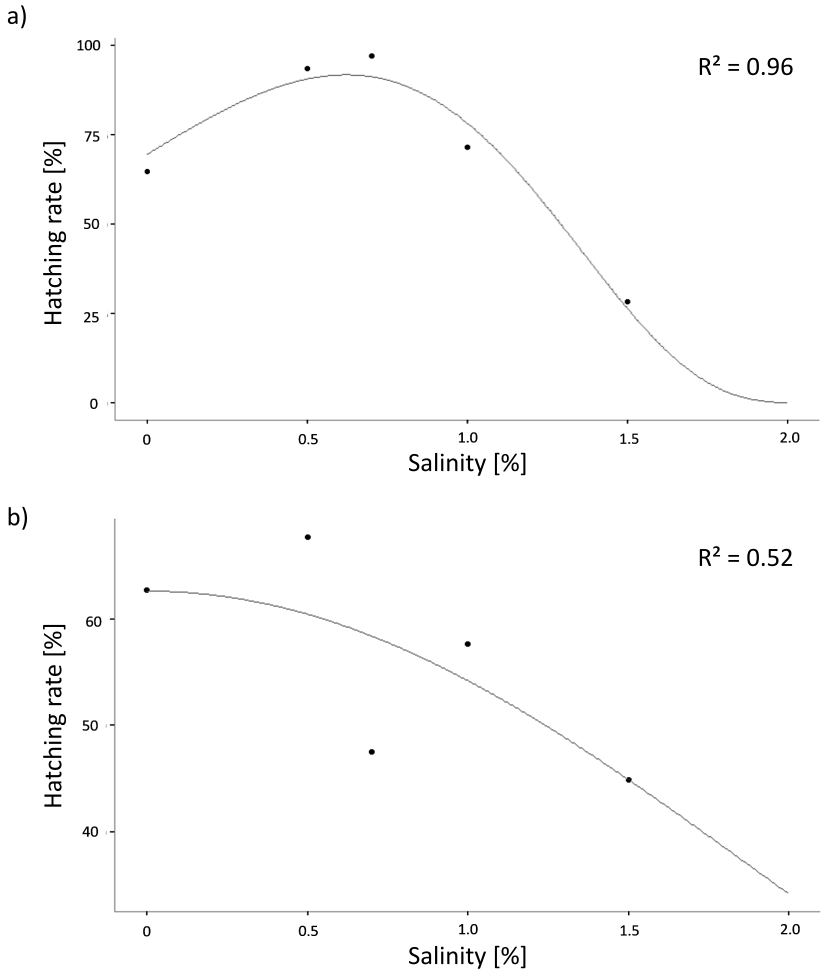

Figure 1. Response curves of hatching rate over salinity for (a) *Sympetrum striolatum* and (b) *S. vulgatum* fitted with the O'Neill function. Consider the different y-axes.

Table 2. Growth rates of *Sympetrum striolatum* and *S. vulgatum* raised in different salt concentrations.

	Salt [%]	Growth rate [mm/d]	R^2
S. striolatum	Tap water	0.032±0.01	0.974
	0.5	0.04	0.997
	0.7	0.04	0.970
	1.0	0.04	0.992
	1.5	0.03	0.985
S. vulgatum	Tap water	0.046±0.01	0.962
	0.5	0.04	0.996
	0.7	0.04	0.987
	1.0	0.05	0.985
	1.5	0.03	0.965

ity (Table 2). There was no significant correlation between salinity and growth rate in our results. As there was only a low number of *S. vulgatum* larvae raised the rates should be interpreted carefully. As larvae were counted weekly when the growth rates were measured, it was noticed that the numbers of *S. striolatum* larvae remained constant over several weeks even though the larvae were kept together in high densities (Fig. 2). Mortality was low in low salinities. However, in the high salinity treatment (1.5%), 85% of the larvae died at the beginning but afterwards the number of larvae remained constant at 15% for nearly two months.

Discussion

Sympetrum striolatum and *S. vulgatum* are ecologically very similar and show different population trends in Europe. We already investigated some possible mechanisms for this (Hogreve & Suhling, 2022): the current population trends may be partly attributed to lowered survival of *S. vulgatum* under drought and by phenological and, thus, size benefits of *S. striolatum*. Additionally, to these mechanisms our results in this study might indicate that the ability of hatching in brackish environments could be more advantageous for *S. striolatum* and therefore future increasing salinity in freshwater habitats might be less challenging for *S. striolatum* compared to *S. vulgatum*.

In our experiment both species had a higher egg survival at slightly increased salt concentration. This effect was most prominent in *S. striolatum*. For *S. striolatum*, low salinity of 0.5% or 0.7% seemed to have little influence or even to be beneficial, as in the case of the hatching rate. For the eggs of *S. striolatum*, the highest hatching rate, i.e., lowest egg mortality, was even recorded in brackish water at 0.7%. At low salinity levels, it could be that a slight disinfecting effect by inhibit bacterial growth had a positive influence on the survival rate of the eggs. Bacteria inhabiting marine and freshwater systems differ slightly physiologically (Hobbie, 1988) and freshwater streams biofilm growth decreased with exposure to salt (Cochero et al., 2017). A salt content of 1.5% resulted in reduced survival of eggs and therefore, at some concentration salt seems to have a negative effect on the development of both species. There may be a limit above about 1% salt content where the salt concentration becomes toxic for the eggs. Also, salt in low concentrations had the effect of reducing or decreasing hatching time in *S. striolatum* and prolonging hatching time in *S. vulgatum*.

As another effect we observed that none of the salt concentrations seemed to have negative effects on larval growth. The growth rates for *S. striolatum* in salty water were slightly higher than in tap water whereas for *S. vulgatum* the rates were similar. It has been proven that at least some Anisoptera are able

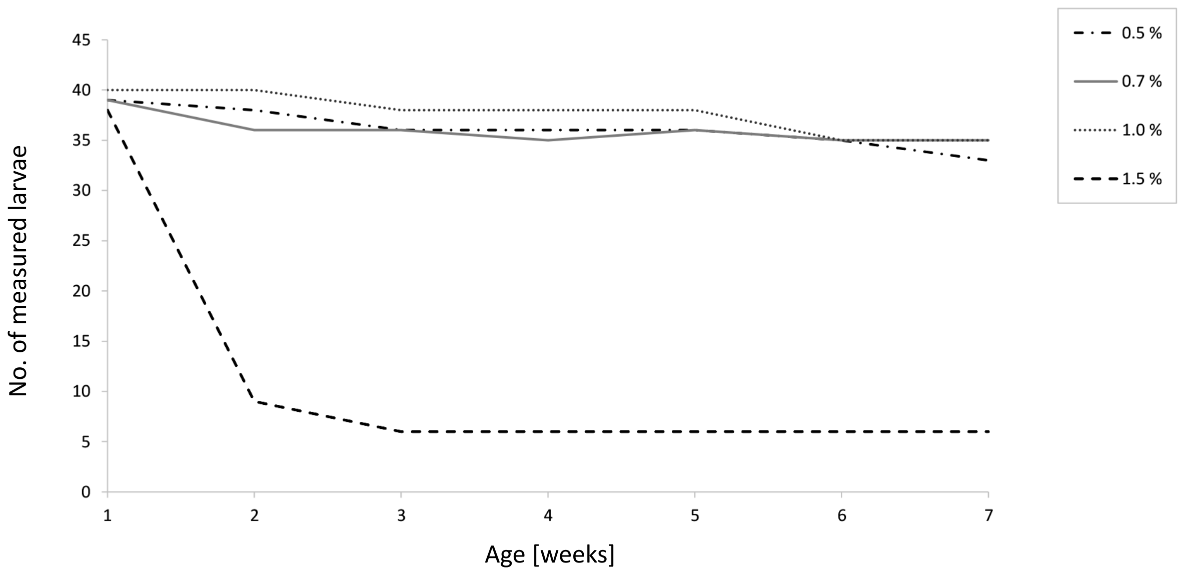

Figure 2. Number of reared larvae of *Sympetrum striolatum* in the same container.

to deal with salty environmental conditions (Komnick, 1982). When dragonfly larvae of *Aeshna cyanea* (Müller, 1764) were transferred to seawater, they re-established a hyperosmotic state compared to their new environment (Komnick, 1982). The increased energy likely required to compensate for increased osmoregulation (Lambret et al., 2021) did not have a negative effect on growth in our experiment. However, it may be that the expected salinity gradient was not found because it is overlaid by the food gradient especially up to 1% salinity which compensated the salt effects. Besides temperature, food and its energy content are the main exogenous factor affecting the growth and development rates of dragonfly larvae (Corbet, 1999; Corbet et al., 2006; Norling, 2021; Suhling et al., 2015). Only sufficient availability and high-quality food allow rapid larval growth (Pickup & Thompson, 1990). The right kind of food can accelerate growth by up to 22% (Hassan, 1976) while too little food leads to underdevelopment and also potentially increased mortality. Feeding with *Artemia* sp. nauplii may be suboptimal, as the *Artemia* only survive for a short time in freshwater. In normal rearing experiments the slow increase of salt content by feeding is usually compensated by frequent water exchanges. Thus, even with daily feeding with *Artemia*, it cannot necessarily be ensured that the dragonfly larvae are optimally supplied with food (Suhling et al., 2015). For the dragonfly larvae reared in brackish water, the *Artemia* nauplii survived for days and therefore food was consistently available for the larvae in the brackish water treatments. Only above 1% the salt seemed to cause other problems as shown by the increasing mortality.

Since *Artemia* sp. survive only a short period in tap water, why were growth rates measured in tap water (Hogreve & Suhling, 2022) almost identical to those in brackish water? Presumably the used food in the tap water did not result in a lower growth rate due to rising intraspecific predation. The larvae compensated the lack of food animals in the tap water with cannibalism. This was noticeable in the astonishing high survival rate of the larvae of *S. striolatum* in this experiment. Significantly higher mortality due to cannibalism was expected due to the high larval densities which were kept together (Anholt, 1994; Johansson, 1996). If the larvae have a choice, they seem to prefer the less dangerous and more defenceless food and pay no further attention to their conspecifics. For experiments in which single larvae are studied, the feeding problem could have a greater impact on the results than in an experimental design in which individuals are kept together, as we did. This could also have an impact on the all over behaviour and cannibalism rates determined so far.

In conclusion the investigated low salt concentrations allow egg development of both species and do not affect the growth rates negatively. If feeding *Artemia* sp. low concentrations of salt added to the water may even improve the food situation. It needs to be investigated if that may also be true for other species than the two tested.

Figure 3. A very relaxed male of *Sympetrum striolatum* – we hope Reinhard is relaxed as well.

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