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# *Coenagrion hastulatum* and *C. lunulatum* – their responses to the liming of acidified lakes and the release of fish (Odonata: Coenagrionidae)

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**Abstract.** The rare and acidification-tolerant *Coenagrion lunulatum* became extinct in Romundstadtjern, a small acidic lake in southern Norway, at some time between 1950 and 1980. The reason was suspected to be liming of the lake to raise the pH level before releasing fish (trout). To substantiate the hypothesis, in 1998–2001 we experimentally limed two other small acidic lakes, Øynaheia A (pH 4.6) and B (pH 4.8), which were also inhabited by *C. lunulatum*. Instead of being made extinct by the liming and the rise of the pH to 7.0, the *C. lunulatum* population at Øynaheia grew strongly during the experimental period. However, when fish (perch) were released later, before 2011, the invertebrate fauna became tremendously impoverished, and *C. lunulatum* was not observed there in 2012, 2014 or 2016. Therefore, liming of lakes does not seem to be a threat to *C. lunulatum*, but the release of fish may probably lead to its extinction. A coexisting population of *C. hastulatum* also grew during the years of liming, but not as much as *C. lunulatum*. However, it survived the introduction of fish, although in low numbers.

**Further key words.** Dragonfly, damselfly, Zygoptera, pH, acidic precipitation, fish predation, Norway, Scandinavia

## Introduction

Acidic precipitation has been a great problem in Scandinavia for several decades, especially in southern Norwegian ecosystems (Rodhe et al. 1995; Hesthagen et al. 1999). Although the precipitation is less acidic now compared to the situation 20–30 years ago, it may take a long time for the water quality and for the fauna and flora of the acidified areas to recover completely; perhaps one hundred years or more, depending on the depth and composition of the soil. The liming of small and large lakes and rivers is therefore still widely practised as a means of raising the pH and restoring and maintaining fish populations in the region (Hindar & Wright 2005).

However, liming of acidic lakes might also have important negative implications, for instance for *Sphagnum* mosses (Eriksson et al. 1983) and acidophilic animals, for instance among Chironomidae (Diptera) and Corixidae (Hemiptera), as mentioned by Degerman et al. (1995). Al Jawaheri & Sahlén (2017) found a negative impact of lake liming on the species richness of Odonata.

The two closely related damselfly species, *Coenagrion hastulatum* (Charpentier, 1825) and *C. lunulatum* (Charpentier, 1840), have a large Palaearctic distribution, from the British Isles eastwards to Sakhalin in Russia (Boudot & Nelson 2015). The more euryoecious *C. hastulatum* is found over large parts of Scandinavia and in most kinds of standing freshwater habitats, whereas *C. lunulatum* has a more eastern distribution and is mostly quite rare; it has often been associated with very or fairly acidic ponds and small lakes with *Sphagnum* edge, especially in north-western Europe (Olsvik & Dolmen 1992; Askew 2004; Boudot & Nelson 2015). In Norway, *C. lunulatum* has been recorded in a few localities in the most northern part, about 20 localities close to the Swedish border in south-eastern Norway, and in a small area further west, in southernmost Norway (Fig. 1). Based on a decrease of available habitat and probably strongly fragmented populations, the national IUCN red list status of *C. lunulatum* is VU – vulnerable (Kjærstad & Olsvik 2015). The status of *C. hastulatum* is LC – least concern.

In one of the few *C. lunulatum* localities in southernmost Norway, Romundstadtjern in Vegårshei, the population went extinct at some time between 1950 and 1980. The species was found there several times between 1930 and 1950, when the pH was measured at approximately 5.5–5.6, but not later, *i.e.*, not in the 1980s and early 1990s (Olsvik et al. 1990; Dolmen 1995). The pH of the lake had decreased because of acidic precipitation over many years, and even though the lake had been limed on at least one occasion before 1980 to reduce the acidity and for the release of fish, the pH was as low as 4.3 in 1980 (Dolmen 1995). However, the lake was limed again between 1980 and 1990, and in 1989 and 1990 the pH had risen to 5.0–5.5 at the time when fish (trout, *Salmo trutta* Linnaeus, 1758) were newly released. Olsvik & Dolmen (1992) initially assumed that acidic precipitation was the most threatening factor for the species. However, since *C. lunulatum* and three other odonate species that disappeared at Romundstadtjern – *Aeshna caerulea* (Ström, 1783), *Somatochlora arctica* (Zetterstedt, 1840) and *Leucorrhinia albifrons* (Burmeister, 1839) – have usually been associated with acidic, peat-bog habitats in Norway, Dolmen (1995) later suggested that the liming might have been the culprit in Romundstadtjern. Many Odonata species seem to tolerate or thrive better in acidic waters than at higher pH. What is more, in studies in southern Sweden (Al Jawaheri & Sahlén 2017), *C. lunulatum* was never recorded in currently limed lakes, only in untreated or previously limed lakes. However, this possible detrimental effect of liming remained unproven. Moreover, since liming of lakes is such a widely used remedy for anthropogenic acidification in Scandinavia, it seemed important to test the hypothesis, that *C. lunulatum* is an acidophilic species and that liming of acidic lakes may affect *C. lunulatum* negatively.

In 1996 and onwards, we got the opportunity to study the effect of liming on *C. lunulatum* as part of a much larger liming project in another area of southernmost Norway: Øynaheia in Froland. On the basis of the above assumptions, we expected the populations of *C. lunulatum* in the lakes to decline significantly after liming. Our hypothesis was that after liming, the *C. lunulatum* population would decline and that the ratio between the density of *C. hastulatum* larvae and the density of *C. lunulatum* larvae in the lakes would change in favour of the more euryoecious *C. hastulatum*.

## Material and methods

### Identification

Larvae of *Coenagrion lunulatum* can best be distinguished from those of the very similar *C. hastulatum* by their more transparent gills and their gill tracheae being much more evenly pigmented and well defined. In *C. hastulatum*, the pigmentation of the tracheae is more uneven and their appearance therefore more 'mottled' (Norling & Sahlén 1997). In addition, large *C. lunulatum* larvae usually have a dense 'coat' of long and short hairs (typically 20–30 hairs or more per segment) on the back of the first few abdominal segments, under the wing sheaths, whereas *C. hastulatum* larvae usually have far fewer and shorter hairs (typically 10–15 or less). There are also other slight differences. Keys with illustrations can be found in Ander (1926),

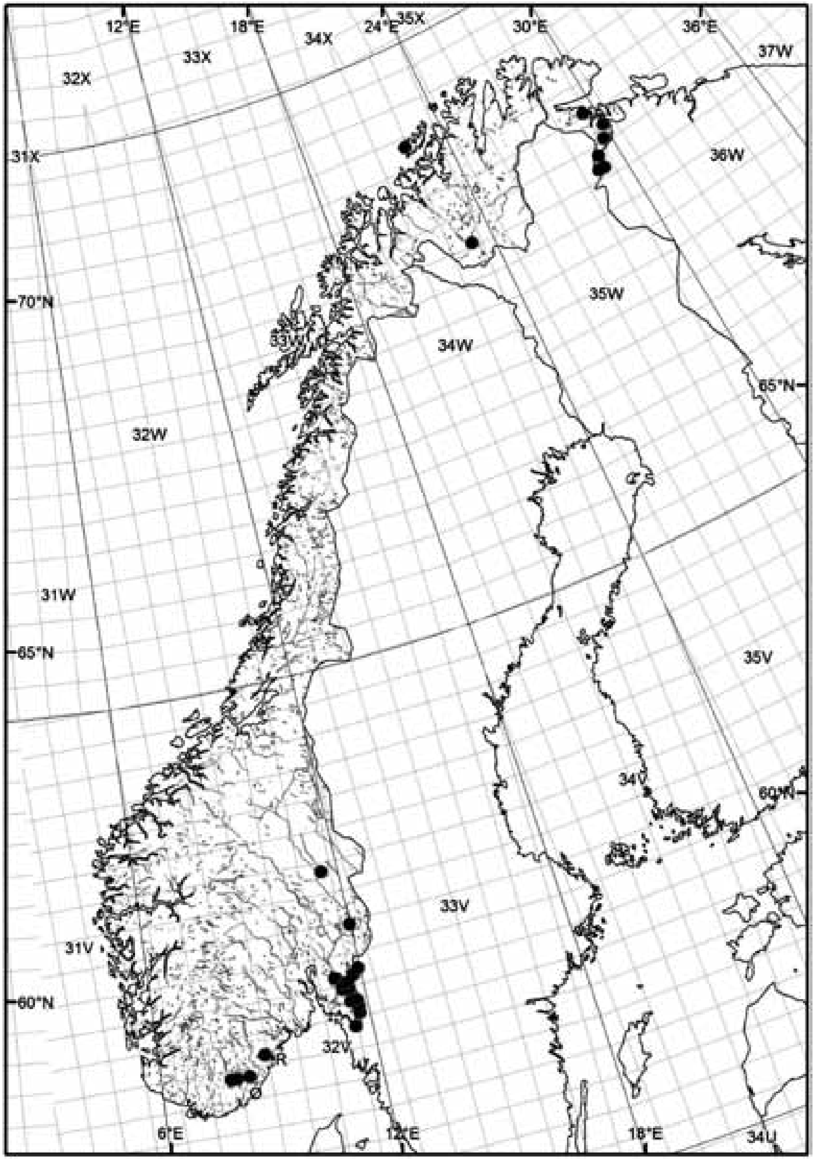

**Figure 1.** Distribution of *Coenagrion lunulatum* in Norway based on 10×10 km UTM squares. Data origin: Olsvik & Dolmen (1992), Artsdatabanken (2016) and H. Olsvik (pers. comm.). R − Romundstadtjern in Vegårshei; Ø − Øynaheia in Froland, where the liming experiment of this study was carried out.

Sahlén (1985), Norling & Sahlén (1997) and Heidemann & Seidenbusch (2002). Some mention that the prementum in the two species differs in size. However, we found this character less useful. Both *C. lunulatum* and *C. hastulatum* are for the most part semivoltine in southern Norway; large, medium-sized (overwintered twice) and small (overwintered once) larvae can all be found in spring. We made use of only large larvae in early May; smaller larvae of the two species can also be distinguished, but less easily (Norling & Sahlén 1997).

## Study area and localities

Fifty-eight acidic lakes in the anthropogenically acidified region Tovdalen in southernmost Norway were investigated for odonate species and other limnic animals. The elevation of the lakes was at 190–295 m a.s.l. and their maximum depths were about 3–4 m. In only two of the lakes, Øynaheia A (Båtsteindammen E of Herefoss) and Øynaheia B (Båtsteintjørna E of Herefoss), at 293 m a.s.l. in Froland, Aust-Agder, we detected the presence of *C. lunulatum*, while *C. hastulatum* was found in all the lakes. None of the lakes had fish.

The bedrock in the area consists mainly of intermediate to acidic gneisses (Sigmond et al. 1984), and the postglacial marine limit (ML) is about 100 m a.s.l. The area belongs to the boreo-nemoral vegetation zone (Moen 1999). The investigated lakes were embedded in *Sphagnum* bogs with scattered rock outcrops, surrounded by woodland or forest (pine *Pinus sylvestris* and spruce *Picea abies*). The situation of the area and the localities are shown in Figure 1. Further information on the lakes involved in the project, their position, size and water quality can be seen in Table 1.

## The liming

The liming started after initial studies of the two localities in 1996 and 1997. Lime was spread on the ice of Øynaheia A each winter/early spring in 1998–2001. About 25–400 kg of powdered limestone (85 % $CaCO_3$) were used, successively more each year, until a pH value of 7.0 was achieved in Øynaheia A, in 2001. Since Øynaheia A drains through Øynaheia B, the latter was also affected by the liming; it reached pH 5.7 at the highest, also in 2001. Two other lakes were chosen as reference localities: Ogge A (a small lake S of Fjer-

**Table 1.** Investigated localities in southern Norway and their geographical positions, sizes and hydrographical data in mid-June or July 1996 before the liming of Øynaheia A and B. Ogge A and Bås C served as reference localities without liming.

| Locality | UTM (32V) | Area [m²] | pH | Cond. ($K_{25}$) [µS/cm] | Colour [mg Pt/L] | $Ca^{2+}$ [mg/L] |
|---|---|---|---|---|---|---|
| Ogge A | MK 460769 | 500 | 4.9 | 23 | 80 | 0.7 |
| Bås C | ML 592070 | 1 300 | 5.0 | 23 | 75 | 0.7 |
| Øynaheia A | MK 651864 | 5 000 | 4.6 | 29 | 60 | 0.7 |
| Øynaheia B | MK 652865 | 13 500 | 4.8 | 35 | 20 | 1.4 |

meros in Iveland) and Bås C (Poddetjørn NW of Kilåsen in Åmli); both were investigated for water quality and odonates, but not limed. The reference lakes had populations of *C. hastulatum*, but not *C. lunulatum*, since we did not know any additional localities for *C. lunulatum* in southern Norway at that time. Further information on the reference lakes can be seen in Table 1.

## Water quality

Water samples were taken in polyethylene bottles at one arm's length from the shore and a depth of 15 cm. pH was determined at the site colorimetrically by a 'Hellige' comparator (indicators: methyl red or bromthymol blue). Water colour was measured by a comparator and Nessler tubes, and conductivity ($K_{25}$) by a Delta Scientific conductivity meter or a WTW Cond. 330i. $Ca^{2+}$ concentration was found by EDTA titration (Titriplex B). Water sampling was carried out in May, June/July and August/September during the pre-liming and liming periods 1996–2001, and also every year later, until 2009, and in addition in 2014.

## Odonata investigations

Investigations of odonate larvae were carried out once a year, in May before emergence of adults had started, in each of the lakes for all sampling years: for Øynaheia A and Øynaheia B in 1997 (pre-liming), 2000 (liming) and 2002–2004 (post-liming). An additional check was done in 2014, after fish had appeared at Øynaheia (see below). Ogge A and Bås C were investigated for odonates only in 1997 and 2000.

Each lake was sampled with a net for odonate larvae using z-sweep sampling in the aquatic vegetation at ten separate, potentially suitable odonate sites along the shore (Dolmen 1991; Skei et al. 2006). Any odonate larvae caught were preserved in 70 % ethanol for later identification. Observations of adult odonates were carried out simultaneously, spending approximately 1 hr at each locality. The Odonata investigations and water sampling took place on the same dates.

The material is preserved at the NTNU University Museum in Trondheim, Norway. Of the odonates recorded, only *C. hastulatum* and *C. lunulatum* are dealt with in the present article.

### Statistics

As the increasing $CaCO_3$ dosages elevated the pH of the two lakes each year during the liming period, the number of both species was tested with the Wilcoxon matched-pairs signed-ranks test (two tailed). This was to track possible changes in their numbers from one year to the next as a response to the elevated pH. The number of larvae in a sample was presumed to mirror the density of larvae in the lake. The 10 z-sweeps per lake were taken at widely separated sites around the lake and have been treated as independent samples. The number of specimens sampled in each locality per sampling date is given as the total and median numbers and range (min–max) of the 10 z-sweeps.

## Results

### Water quality

The hydrographical environment in the two lakes (Øynaheia A and Øynaheia B) throughout the experimental period, as described by the $Ca^{2+}$ concentration and the pH, can be seen in Figure 2.

### The pre-liming period (1996–1997)

The $Ca^{2+}$concentration of the two lakes before liming varied between 0.5 and 1.6 mg/L, and the pH was around 4.6–5.1. The lowest pH values were usually recorded in May and September. For the reference localities (Ogge A and Bås C), the $Ca^{2+}$concentration was measured at 0.7–1.4 mg/L and the pH values around 4.6–5.4. The water colour varied a lot within each locality throughout the season, and also from one locality to another. Øynaheia A and Øynaheia B had relatively clear water (10–60 mg Pt/L), while Ogge A and Bås C had more brownish water (45–150 mg Pt/L).

## The liming period (1998–2001)

The liming of Øynaheia A and Øynaheia B had a strong impact on the water chemistry, with highly elevated values of $Ca^{2+}$concentration and pH. The $Ca^{2+}$concentration peaked in the third and fourth years of liming, when the dosage of powdered limestone was also highest. In 2001, the increase of $Ca^{2+}$ in Øynaheia A was more than 6 mg/L (increase from <1 mg/L to 7.1 mg/L). In Øynaheia B, the increase was much less, but still distinct. The increased

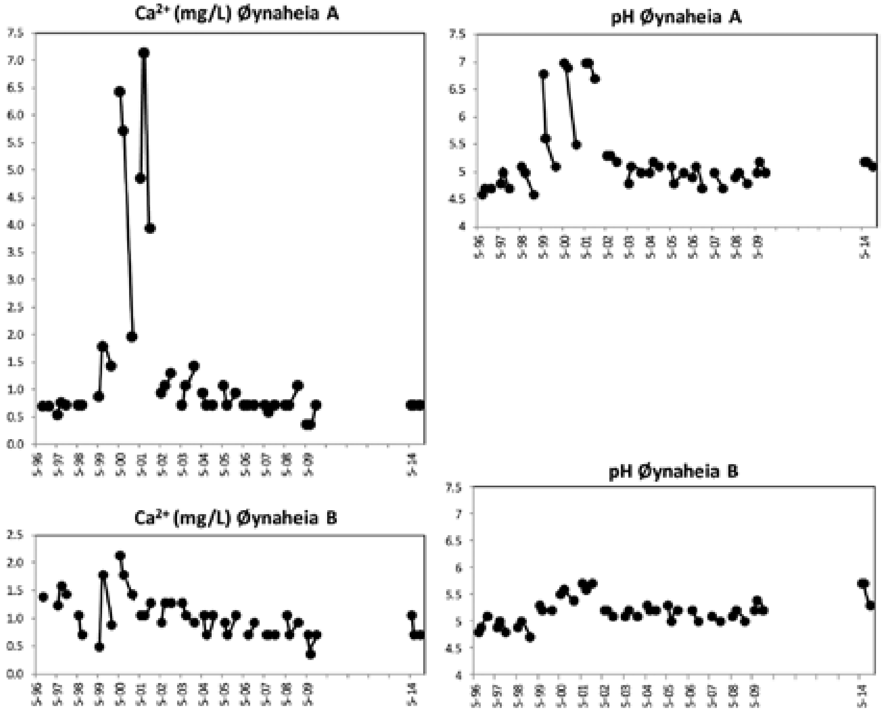

**Figure 2.** The $Ca^{2+}$ concentration and pH in two lakes in southern Norwax, Øynaheia A and B in Froland, throughout the experimental period of this study (1996–2014). Liming was carried out every spring from 1998 to 2001.

$Ca^{2+}$concentration was accompanied by a considerable elevation of the pH. The highest pH values were as a rule achieved in spring, after which they fell, often strongly. The maximum value (pH 7.0) was obtained at Øynaheia A in 2000 and 2001, while Øynaheia B reached 5.7. The reference localities (Ogge A and Bås C) showed no obvious changes in the $Ca^{2+}$ concentration or the pH. The water colour varied, as before, during the four years of liming, except that the water became more brownish at Øynaheia A and Øynaheia B.

### The post-liming period (2002–2009, 2014)

After the four years of liming, the pH of the limed lakes had decreased again in 2002, but was still somewhat higher than the pre-liming level, and stayed like that for the rest of the post-liming period (2002–2009 and 2014). There was probably a weak, natural increase in the pH values at all localities throughout the period, as implied by the reference localities (Fig. 3). The water colour varied within approximately the same boundaries as in the liming period.

### *Coenagrion hastulatum* and *C. lunulatum*

From very low numbers of *C. lunulatum* larvae in Øynaheia A (total 7, median 0.5, range 0–2) and Øynaheia B (tot. 2, med. 0, range 0–2) in May 1997, the numbers rose and in 2000 (third year of liming) had increased significantly ($P < 0.01$) at both localities seen together (Fig. 4). In 2002, the first post-liming year, the number had increased even more. There are no data from Øynaheia B in 2002. This increase continued, and when we finished our regular damselfly studies, in 2004, the numbers of larvae had risen to as many as tot. 132, med. 10.5, range 4–40 and tot. 51, med. 5, range 0–14, respectively, in Øynaheia A and Øynaheia B.

*Coenagrion hastulatum* showed a similar increase from low numbers in 1997 (Øynaheia A: tot. 33, med. 1.5, range 0–17 and Øynaheia B: tot. 9, med. 1, range 0–3) to 2000, which was significant for both localities ($P < 0.05$ and $P < 0.01$, respectively; Fig. 5). Except for a decrease ($P < 0.01$) at Øynaheia A in 2003, the trend was still an increase in the number of larvae, although not as strong as in *C. lunulatum*. In 2004, the numbers were tot. 260, med. 24.5, range 4–57 and tot. 83, med. 7.5, range 0–25 for Øynaheia A and Øynaheia B.

Although *C. hastulatum* was usually much more numerous in the samples than *C. lunulatum*, the general trend for both localities during and after the liming years was that the ratio between the numbers of *C. hastulatum* and *C. lunulatum* larvae decreased, as shown by the line y = -0.54x (Fig. 6).

In the reference localities, Ogge A and Bås C, there were no significant changes in the number of *C. hastulatum* larvae between 1997 and 2002 (Ogge A in 1997: tot. 58, med. 2, range 0–16 and in 2000: tot. 42, med. 4,

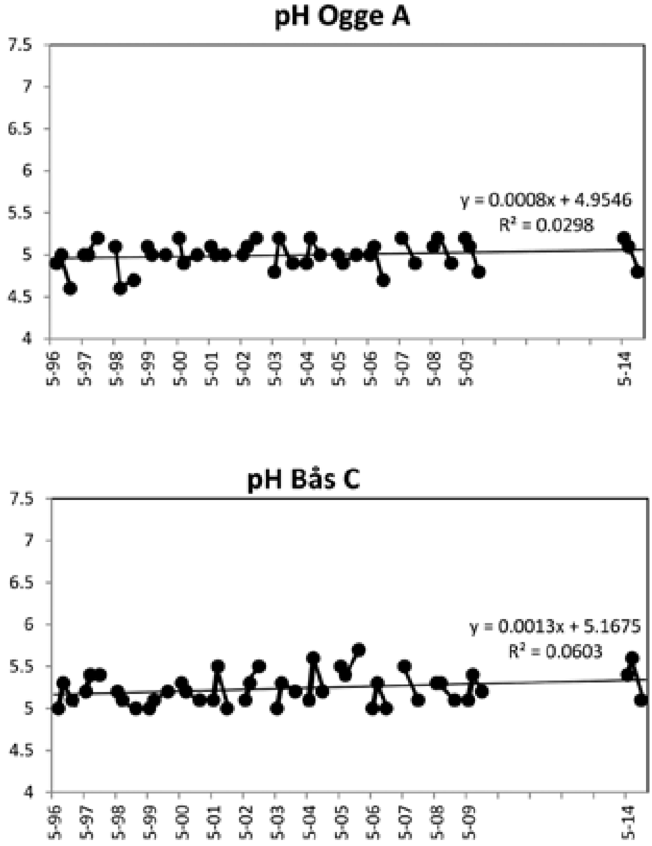

**Figure 3.** The trend in the pH values in the two lakes in southern Norway used as reference localities, Ogge A in Iveland and Bås C in Åmli, throughout the experimental period (1996–2014). In both localities, a slight, natural increase in pH can just be perceived.

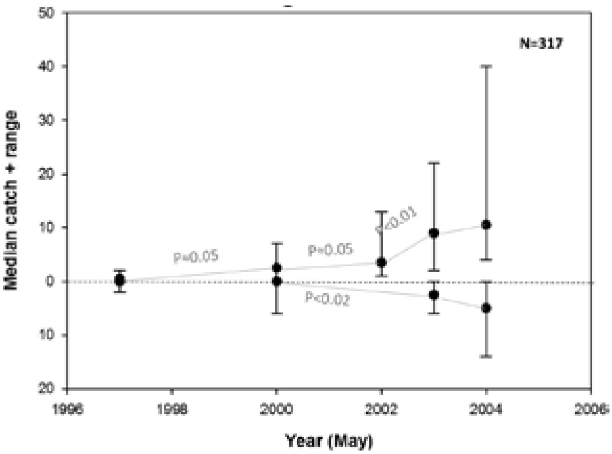

**Figure 4.** Increase in the median number and range of *Coenagrion lunulatum* larvae in 10 sweep samples on each date, in two lakes in southern Norway throughout the experimental period of this study (1996–2014). Liming was carried out every spring from 1998 to 2001. Øynaheia A above the dotted zero line, Øynaheia B below; data for Øynaheia B in 2002 is missing.

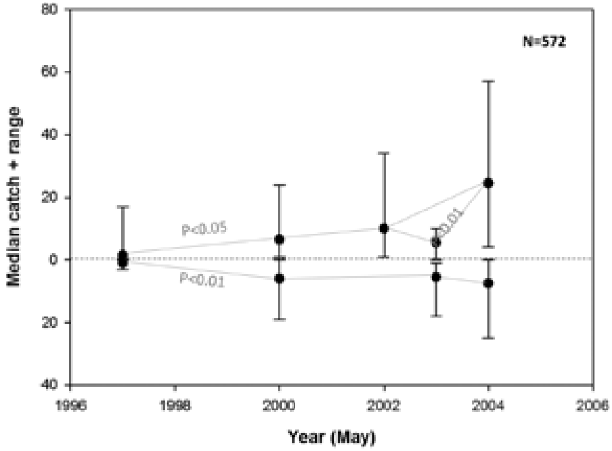

**Figure 5.** Increase in the median number and range of *Coenagrion hastulatum* larvae in 10 sweep samples on each date, in two lakes in southern Norway throughout the experimental period of this study (1996–2014). Liming was carried out every spring from 1998 to 2001. Øynaheia A above the dotted zero line, Øynaheia B below; data for Øynaheia B in 2002 is missing.

range 1–7; Bås C 1997: tot. 32, med. 3, range 0–6 and in 2000: tot. 63, med. 5.5, range 0–17).

## Fish

In 2011, several shoals of small perch *Perca fluviatilis* Linnaeus 1758 (3–4 cm) were seen for the first time, and the invertebrate fauna had already become markedly impoverished. The localities were visited again in spring and/or early summer in 2012, 2014 and 2016. On these occasions, a very few individuals of *C. hastulatum* were seen on the wing, and also a few other odonate species, but no *C. lunulatum*. In early May 2014, a total of 12 perch, 12–13 cm long, were found dead in the water along the edge of Øynaheia A, and several more were seen alive. This demonstrates the large stock of fish in the lakes. In 10 z-sweeps in each of the two lakes, only one *Coenagrion* sp. larva was caught in Øynaheia A and zero in Øynaheia B. If the results from the two lakes are combined, numbers are significantly lower (P <0.05) than those in 1997, before the liming started and when the number of *C. lunulatum* larvae was at its lowest. The difference in part of the macro-invertebrate fauna in the lakes before and after the introduction of fish can be seen in Table 2.

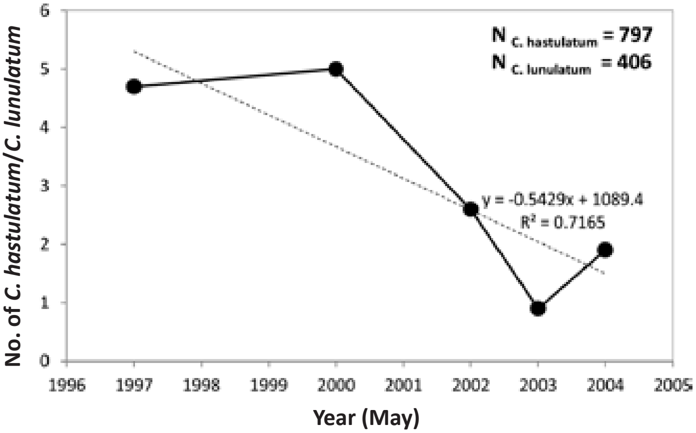

**Figure 6.** The changing ratio between the numbers of *Coenagrion hastulatum* and *C. lunulatum* larvae in catches in two lakes in southern Norway throughout the experimental period of this study (1996–2014), in favour of *C. lunulatum*.

**Table 2.** Number of individuals from four insect orders, caught in 10 z-sweeps per locality in two lakes in southern Norway, in May 1997 (before fish introduction and before liming) and in May 2014 (after fish introduction). A – Øynaheia A; B – Øynaheia B; / – either or.

| Taxon | A (1997) | A (2014) | B (1997) | B (2014) |
|---|---|---|---|---|
| **Ephemeroptera** (larvae) | | | | |
| Leptophlebiidae | 66 | 1 | 57 | 2 |
| **Odonata** (larvae) | | | | |
| *Coenagrion hastulatum* | 33 | 0 | 9 | 0 |
| *C. lunulatum* | 7 | 0 | 2 | 0 |
| *C. hastulatum/lunulatum* | 8 | 1 | 2 | 0 |
| *Aeshna juncea* | 6 | 0 | 13 | 0 |
| *Ae. grandis* | 1 | 0 | 5 | 0 |
| *Aeshna* sp. (small) | 13 | 0 | 7 | 0 |
| *Libellula quadrimaculata* | 1 | 2 | 1 | 4 |
| *Leucorrhinia dubia* | 18 | 0 | 17 | 0 |
| *Leucorrhinia/ Sympetrum* sp. (small) | 1 | 0 | 0 | 0 |
| **Hemiptera** | | | | |
| *Notonecta glauca* (adult) | 0 | 0 | 1 | 0 |
| *N. lutea/reuteri* (larvae) | 312 | 0 | 103 | 0 |
| Corixidae (adult *Sigara distincta*, *S. semistriata*, *Cymatia bonsdorffi*) | 9 | 1 | 6 | 0 |
| **Coleoptera** | | | | |
| Dytiscidae (adult *Hygrotus inaequalis*, *Rhantus exsoletus*, *Acilius sulcatus* | 16 | 0 | 12 | 0 |

## Discussion

In the introduction, we mentioned that *Coenagrion lunulatum* is associated with very or fairly acidic ponds and lakes, at least in its north-western European distribution, and that elevation of the pH by liming was thought to have made the species extinct in the acidic lake, Romundstadtjern, in southernmost Norway (Dolmen 1995; *cf.* Olsvik et al. 1990). The link between *C. lunulatum* and low pH was previously established by Schmidt (1978) and McGeeney (1986), and our own experience from Norway is also unambiguous: the pH of 12 *C. lunulatum* localities in south-eastern Norway, all listed by Olsvik & Dolmen (1992) varied from ≤4.4 to 5.8 (Fig. 7). In southern Sweden, Al Jawaheri & Sahlén (2017) never found the species in currently limed lakes.

We therefore hypothesized that it was not the ongoing anthropogenic acidification in Scandinavia, but rather the liming of lakes, that was the biggest problem for *C. lunulatum* (Dolmen 1995). This idea was partially supported by Nelson et al. (2000), who stated that eutrophication seemed to be the most serious threat to *C. lunulatum* (see also Boudot & Nelson 2015). Not only an increased supply of plant nutrients, but also a slight increase in pH, for instance by the liming of a lake, can lead to eutrophication (Fondriest Environmental Inc. 2016).

Against this background, we expected the populations of *C. lunulatum* to decline after the experimental liming of two other lakes, Øynaheia A and Øynaheia B. Moreover, since *C. hastulatum* was also present, we predicted a change in the relationship between the numbers of *C. hastulatum* and *C. lunulatum* in favour of the more euryoecious *C. hastulatum*.

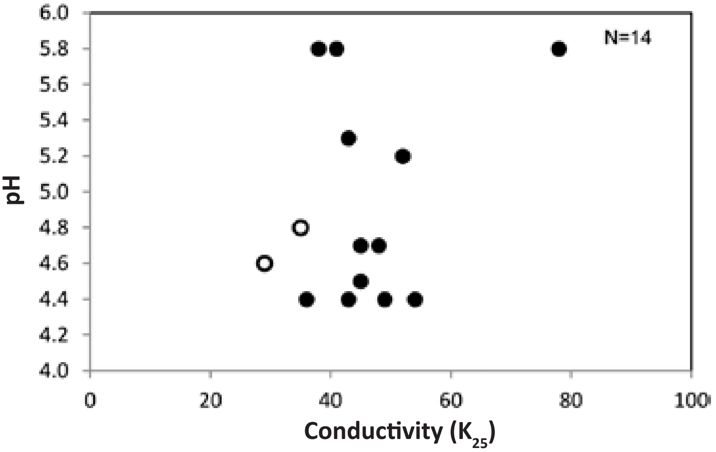

**Figure 7.** pH and conductivity [µS/cm] at 14 *Coenagrion lunulatum* localities in south-eastern and southernmost Norway. The 12 first-mentioned localities in Olsvik & Dolmen (1992) are marked with filled circles. In addition, the two lakes at Øynaheia (1996, *i.e.*, before liming) are marked with open circles. pH and conductivity values 1989–1990: DD, unpubl. data.

Hence, the results of the present liming experiment were highly unexpected. There was no sign that any of the year-classes of *C. lunulatum*, which experienced the liming for shorter or longer periods, suffered any harm from it; rather the contrary. Already from the first samples we took after the first liming, and throughout the four-year liming period, and after, the numbers of *C. lunulatum* and *C. hastulatum* rose significantly, especially *C. lunulatum*. This increase took place in both limed lakes. No significant changes could be seen over the same period for *C. hastulatum* in the two reference localities.

From the liming experiment it is clear that an elevated pH level, from very acidic to about neutral, was an advantage for both *Coenagrion* species, and apparently more so for *C. lunulatum* than for *C. hastulatum*. However, the mechanisms behind the increased population growth are not clear, *e.g.*, whether it was physiological or ecological. Within certain limits, continually higher pH may better meet specific physiological needs of the larvae and give them continually better living conditions, or at least an optimal threshold pH is achieved. Alternatively, the population growth may simply be the result of a higher abundance of prey animals and therefore resulting in a better survival of the odonates. Under such circumstances, the population growth will continue until carrying capacity is reached both in the water and on land.

The results are in direct contrast to those of Foster's (1995) investigations, where it was found that liming of peat pools in the Loch Fleet catchment in Scotland had no effects on the population densities of Odonata, Hemiptera and Coleoptera, and also to Johansson & Brodin's (2003) results for *C. hastulatum* in northern Sweden.

*Coenagrion lunulatum* in southern Norway, and supposedly also in the rest of north-western Europe, is therefore not dependent on acidic water, but can easily tolerate neutral pH values. The species even seems to profit from a rise from acidic to neutral conditions, more than *C. hastulatum*. This amplitude of tolerance can likewise be mirrored in the aquatic habitat of the species in Central Europe, which is not acidic, but within a wide range of biotopes like cattle ponds, gravel pits and clay pits, etc., and also slightly more eutrophic water bodies (Heidemann & Seidenbusch 2002; Boudot & Nelson 2015). Thus, there is apparently a geographical habitat shift between the Central European and the north-western populations of *C. lunulatum*. However, this is probably not caused by physiological differences but is due to a combination of available habitats and other, more subtle, ecological factors.

Why then did *C. lunulatum* disappear from Romundstadtjern after the 1950s? One possibility is that the extreme acidity measured around 1980 (pH 4.3) may have been too much even for *C. lunulatum* (see Olsvik et al. 1990). However, although there are interspecific differences, Odonata larvae in general tolerate quite acidic water (Hudson & Berrill 1986; Pollard & Berrill 1992; Carbone et al. 1998; Corbet 2004; Al Jawaheri & Sahlén 2017) and Rychła et al. (2011) found that only pH values below 3.0 had a detrimental effect on investigated odonates.

Another possibility is that the introduced predatory fish (trout, after the lake had been limed) decimated the *C. lunulatum* population to such a degree that it went extinct. In either case, *C. lunulatum* is a rare species, and no other localities existed in the vicinity from where recolonization of *C. lunulatum* to Romundstadtjern could take place.

The fish hypothesis is supported by what also happened at Øynaheia A and B. After fish (perch) had appeared, the invertebrate fauna and diversity became extremely poor, and *C. lunulatum* was never recorded again. The pH was measured at 5.2 and 5.7, respectively, which should suit *C. lunulatum* well.

That various fish species can reduce the density of Odonata larvae considerably by predation, maybe even to extinction, has been pointed out by, *e.g.*, Eriksson et al. (1983), Henrikson (1988), Carbone et al. (1998), Johansson & Brodin (2003), Rychła et al. (2011) and Al Jawaheri & Sahlén (2017). That some odonate species, especially the more active ones, like *Leucorrhinia* spp. (and also like *Coenagrion* spp.), are more vulnerable than others to fish predation, has also been documented (Eriksson et al. 1980; Henrikson 1988; Johansson et al. 2006). However, at Øynaheia A and B, unlike *Coenagrion* spp. and many other invertebrate species, the less active and more cryptic species, *Libellula quadrimaculata* Linnaeus, 1758, showed no signs of decrease in abundance after the introduction of fish there (Table 2).

The vulnerability of odonates may also depend on which fish species are present; for example, perch had a greater impact on the odonate fauna than seven other common freshwater fishes (Wittwer et al. 2010; see also Wohlfahrt et al. 2006). However, trout and other salmonids are also known to be heavy predators on odonates (CORBET 2004; JOHANSSON et al. 2006; WITTWER et al. 2010).

The high density of perch at Øynaheia A and B had had a tremendously negative effect on the invertebrate fauna. Under such conditions some species sensitive to predation can become so reduced in number that they are impossible to detect, and if there is no immigration of new individuals, the populations may even become extinct.

Some authors emphasize that *C. lunulatum* inhabits small, and for the most part shallow, water bodies (*e.g.*, HEIDEMANN & SEIDENBUSCH 2002; BOUDOT & NELSON 2015). This habitat choice corresponds well with the fact that *C. lunulatum* is an early flier, since small water bodies are more quickly heated up in spring. However, it is also possible that the habitat choice is an adaptation to the vulnerability to fish predation by the species, since small, shallow water bodies less frequently have fish.

## Conclusions

*Coenagrion lunulatum* was most probably not made extinct in Romundstadtjern because of liming of the lake. Although the species has high tolerance to acidic water, it could possibly have been the extreme pH situation around 1980 (pH 4.3) that caused its extinction. However, a more probable explanation is the introduction of predatory fish (trout) to the lake. This conclusion was substantiated by the experimental liming of two other lakes, Øynaheia A and B, where the *C. lunulatum* population grew strongly during the years of liming, but eventually went extinct when fish (perch) were released. Liming of acidic lakes, at least in the way it is carried out in Scandinavia, seems therefore not to be a threat to *C. lunulatum,* although the subsequent release of fish after liming may be detrimental.

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