Winter compensatory growth under field conditions partly offsets low energy reserves before winter in a damselfly

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Despite the survival value of high energy reserves during winter, animals often face energy deficits when entering winter. Compensatory growth in energy reserves during the winter period to buffer such deficits may increase winter survival and alleviate the need for costly compensatory mechanisms before or after winter when predation risk is much higher. However, such compensatory responses in energy reserves during winter have not been demonstrated under field conditions. We explored if *Lestes eurinus* damselfly larvae can compensate for suboptimal energy reserves during winter at 4°C when their ponds are covered with ice. In a field enclosure experiment, we demonstrated compensatory growth in terms of body mass and energy reserves in larvae whose energy status was previously manipulated in the laboratory. These results were supported by patterns in body mass and energy reserves over winter in two natural unmanipulated populations. Winter survival was high overall and not affected by compensatory growth. We hypothesize that the observed compensatory growth in energy reserves during winter may shape life history decisions in autumn and spring, and may make resource availability during winter as or more important than energy reserves before winter.

Many animals living in seasonal environments and which do not migrate experience winter as a particularly harsh period. Many species enter diapause to pass the environmental rigors of winter periods, while others must simply withstand these harsh conditions (Danks 1991, Leather et al. 1993). For both these strategies reduced energy intake is a necessary consequence of winter, and most organisms have a reduced metabolism and undergo other physiological changes to reduce energy demands (Sokolov 1980, Tauber et al. 1986, Lee and Denlinger 1991). However, even a low metabolism depletes energy reserves, and this becomes especially important when the adverse conditions are prolonged (Tauber et al. 1986, Ellers and Van Alphen 2002). As a result, winter survival has been shown to be dependent upon energy reserves before winter in several taxa, including fish (Schultz and Conover 1999, Biro et al. 2004) and insects (Han and Bauce 1998, Irwin and Lee 2000, Ellers and Van Alphen 2002). Even if animals survive the winter, the lowered energy reserves at the end of the winter may persist into the next summer season

and reduce fitness (Irwin and Lee 2000, Ellers and Van Alphen 2002).

Despite the obvious survival value of building high energy reserves before the winter, this may conflict with several other processes. For example, exposure to predators has been shown to result in lower levels of energy reserves (Scheuerlein et al. 2001, Pratt and Fox 2002, Garvey et al. 2004, Stoks et al. 2005a, 2006b). Also under time constraints imposed by seasonality, animals may accumulate less energy (Rolff et al. 2004, Stoks et al. 2006a, 2006b). As a result, many organisms may enter the winter with inadequate energy reserves. Given that the relative importance of stressors like predation is likely less intense during the winter, we hypothesize that animals may show compensation during winter conditions for such suboptimal energy reserves.

Although compensatory growth in terms of energy reserves is widespread under non-winter conditions (Nicieza and Metcalfe 1997, Morgan and Metcalfe 2001, Stoks et al. 2006a), under winter conditions it has only been shown in laboratory studies of fish

(Metcalfe and Thorpe 1992, Bull and Metcalfe 1997). One study showed compensatory growth in terms of mass during winter field conditions (Alvarez and Nicieza 2005). However, compensatory growth in terms of mass may not reflect compensatory growth in terms of energy reserves and both may be even traded off against each other (Forsman and Lindell 1991). Whether compensatory growth in terms of energy reserves also occurs under winter field conditions is unknown. Identification of compensatory mechanisms in terms of energy reserves during the winter is, however, important as it may increase winter survival and alleviate selection on costly compensatory mechanisms before and after winter when predation risk is likely to be much higher.

We set out to test for the presence of compensatory growth in energy reserves during winter under field conditions in an invertebrate: larvae of the damselfly *Lestes eurinus*. *Lestes eurinus* eggs are laid in summer and hatch into the aquatic larval phase of the life cycle within a few weeks. Larvae grow rapidly over the autumn months, overwinter under the ice at northern latitudes, and complete the larval stage the next spring (Lutz 1968, Paulson and Jenner 1971). *Lestes eurinus* occurs in permanent water bodies without fish across eastern North America, where large dragonfly larvae are top predators (Stoks and McPeek 2003, 2006). In New England ponds, where this study was conducted, ponds are typically covered with ice from late November until early April. During this period, animals experience water that is continuously 3–4°C. Compensatory growth in terms of energy reserves has been shown in another *Lestes* species under spring and summer conditions in the laboratory (Stoks et al. 2006a). Energy is often stored as carbohydrates for short-term use (immediate source of energy for metabolism and activity). The capacity of many insects to store polysaccharides is, however, limited and carbohydrates that are ingested above the immediate caloric requirement are often converted to lipids, which serve as long-term energy stores (e.g. energy for metamorphosis, egg production) (Klowden 2002). In insects, typical carbohydrate reserves are glycogen, trehalose and glucose (Klowden 2002). Preliminary measurements indicate that in damselfly larvae, trehalose concentrations are <10% of free glucose concentrations (McPeek unpubl.), so these were not measured. The predominant lipid for energy storage in insects is in the form of triglycerides (Klowden 2002). Therefore, we focused on glycogen, glucose and triglycerides when assessing energy storage pools (see also Stoks et al. 2005a). Given the short- and long-term importance of energy reserves, we expect larvae that enter winter conditions with lower energy reserves either to compensate for this poor start by acquiring more energy while under the ice, or to have higher mortality rates as a consequence of

their initial energy deficit. We evaluated the presence of compensatory growth in mass and in energy reserves under winter field conditions both by comparing natural unmanipulated populations and by performing a field enclosure experiment with larvae whose energy levels were previously manipulated in the laboratory.

Methods

Field monitoring

To obtain background information on the natural in situ patterns in growth rate and energy reserves, and phenomenological evidence for the occurrence of winter compensatory growth, we monitored growth rates of *L. eurinus* throughout larval development and changes in energy reserves during winter in Hemphill Pond and Sylvester Pond (VT, USA). Per pond, larvae were collected at four key points in the larval phase: when freshly hatched (15 August 2004), before winter (11 November 2004), after winter (28 April 2005), and in the last instar before emergence (3 June 2005).

To quantify growth rate, dry masses of 17 to 30 larvae per sampling date and population were obtained by drying the larvae for 48 h at 60°C and weighing them to the nearest 0.01 mg using an electrobalance. Growth rate between two successive sampling dates was calculated as (ln(mean mass at sampling date $i+1$)− ln(mean mass at sampling date i)) divided by the number of days between both sampling dates. To quantify changes in energy reserves during winter, 15 larvae of the samples before and after winter were stored individually in microcentrifuge tubes in a −80°C freezer and the amounts of free glucose, glycogen and triglycerides in each larva were later quantified colorometrically on total homogenates. Analyses of energy reserves were performed within one month after collection. For a detailed description of the protocols see Stoks et al. (2005a).

Enclosure experiment

To directly evaluate the ability of larvae to compensate during the winter for energy deficits before the winter, an experiment in field enclosures was performed with larvae whose energy reserves were manipulated prior to the winter. In a first step, energy reserves of field-collected larvae were manipulated in the laboratory. For this, 155 larvae of *L. eurinus* were collected in Hemphill Pond on 16 November 2004. Larvae were brought to the laboratory and placed individually in plastic cups (5 cm ⌀, 9 cm height) in an incubator at 5°C, the water temperature of the pond at that time. Because larvae have a higher metabolism at higher temperatures, temperature in the incubator was increased to 16°C

over 24 h to manipulate energy reserves. Each larva was randomly assigned to one of three food treatments: (1) high food: one ration of brine shrimp each morning and evening, (2) intermediate food: one ration of brine shrimp every second day in the morning, and (3) no food: starvation. Feeding treatments continued for six days. The number of brine shrimp given on each feeding occasion to a single larva was 223 ± 28 (mean ± 1 SE; n = 6). After six days, temperature was again decreased to 5°C over 24 h. Wet masses of all larvae were measured to the nearest 0.01 mg after gently blotting larvae dry with absorbent tissue. To assess the impact of the manipulation, 15 larvae per treatment group were immediately sacrificed and stored individually in microcentrifuge tubes in a −80°C freezer for analyses of energy reserves before the winter.

Winter compensatory growth of these manipulated larvae was then tested in field enclosures. For this, larvae of the high (n = 36), intermediate (n = 36) and no (n = 37) food treatment group were placed in individual enclosures on 23 November (total of 109 uniquely numbered enclosures). For logistic reasons this was done in Sylvester Pond. Each enclosure consisted of a plastic framework ($9 \times 9 \times 6$ cm) covered with a small bag made of nylon mosquito netting (1.1×1.1 mm mesh size). Previous experiments have shown that enclosures with this mesh size are quickly invaded by many invertebrate taxa (e.g. copepods, cladocerans, amphipods, ephemeropterans, annelids) (Stoks and McPeek 2003). The enclosures were randomly attached to a rope with cable ties and lowered to the bottom of the pond (ca 2 m). Throughout the experiment, temperatures were recorded every hour using a temperature logger. Enclosures were removed from the pond on 13 April 2005, the first day the pond was free of ice. Larvae were immediately returned to the laboratory, their wet mass was measured to the nearest 0.01 mg, and they were stored at −80°C. Individual growth rate was calculated as [ln(mass after winter)− ln(mass before winter)]/141 d. After the winter, we randomly selected 15 larvae per treatment for analysis of energy reserves.

Statistical analysis

We tested for effects of treatment factors [depending on the experiment: population (Hemphill Pond and Sylvester Pond), food manipulation (high, intermediate and no food) and timing (before and after winter)] on levels of energy reserves using MANCOVAs with mass as a covariate. The structure of this analysis ensures that the effect of treatment factors is assessed using mass-corrected levels of energy reserves. Further, this mass correction ensures that compensatory growth in mass and compensatory growth in energy reserves are

independent from each other. Levels of energy reserves and mass were ln(transformed) to meet model assumptions. To interpret the MANCOVA results, we also performed separate ANCOVAs per energy reserve pool. To compare means between food manipulation levels we used Tukey posthoc tests. All models were run using Statistica 6.0. Note that for the figure we plotted mass-corrected energy reserve levels calculated by dividing levels by larval wet mass. This enables comparison among studies as opposed to presenting least squares means.

Results

Field monitoring

Between egg hatching and the onset of winter, growth rates were high in both Sylvester Pond and Hemphill Pond (Fig. 1a). As growth rate during autumn was
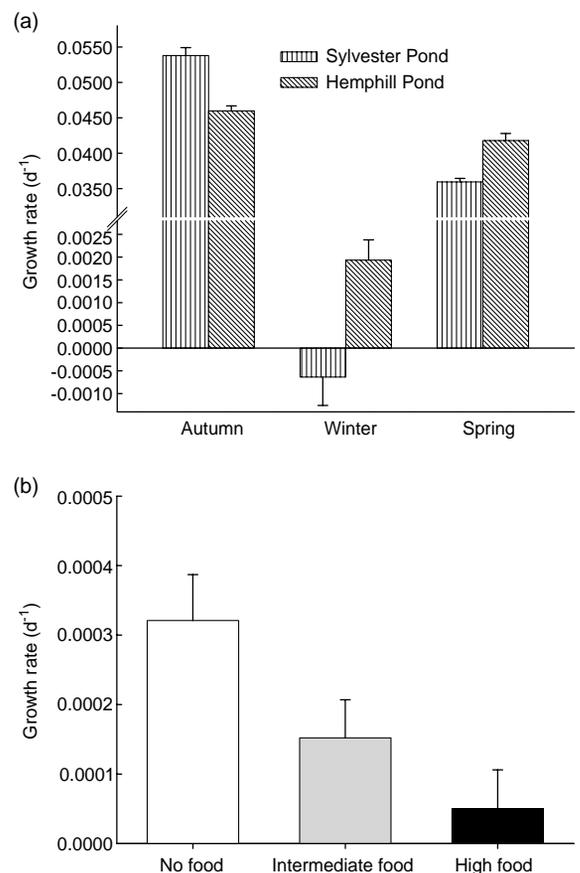

Fig. 1. Growth rate in terms of body mass of *Lestes eurinus* (a) during autumn, winter and spring in the field monitoring in Sylvester and Hemphill Pond, and (b) during winter for the different food treatments in the field enclosure experiment in Sylvester Pond. Means are given with 1 SE.

higher in Sylvester Pond than in Hemphill Pond (t-test, $t_{36} = 6.10$, $p < 0.0001$; Fig. 1a), larvae in Sylvester Pond had a higher mass when they entered winter (Sylvester Pond: 6.13 ± 0.58 mg [mean ± 1 SE]; Hemphill Pond: 2.97 ± 0.19 mg [mean ± 1 SE]) (t-test, $t_{36} = 5.65$, $p < 0.0001$). During winter, growth rates were very low in both ponds, but lower in Sylvester Pond than in Hemphill Pond (t-test, $t_{58} = -3.35$, $p < 0.01$; Fig. 1a). After winter, growth rates in both ponds were high again, but still lower in Sylvester Pond (t-test, $t_{56} = -5.16$, $p < 0.0001$; Fig. 1a). In each period, growth rates were significantly higher than zero, except during winter in Sylvester Pond (one-sample t-test, Sylvester Pond during winter: $t_{29} = -1.02$, $p = 0.32$; all other $p < 0.0001$).

Mass-corrected energy reserve levels changed during winter and this change depended on population (MANCOVA, population: $F_{3/52} = 6.81$, $p < 0.001$; timing: $F_{3/52} = 22.95$, $p < 0.0001$; population $\times$ timing: $F_{3/52} = 4.30$, $p < 0.01$). Before winter, levels of the energy reserves were higher in larvae from Sylvester Pond compared to larvae from Hemphill Pond (Tukey test, all $p < 0.05$; Fig. 2). During winter, levels of glucose increased in a uniform way in both populations (ANCOVA, population: $F_{1/55} = 6.85$, $p < 0.05$; timing: $F_{1/55} = 14.24$, $p < 0.001$; population $\times$ timing: $F_{1/55} = 1.80$, $p = 0.19$; Fig. 2a). Levels of glycogen decreased during winter for larvae from Sylvester Pond, but increased for larvae from Hemphill Pond (ANCOVA, population $\times$ timing: $F_{1/54} = 4.62$, $p < 0.05$;
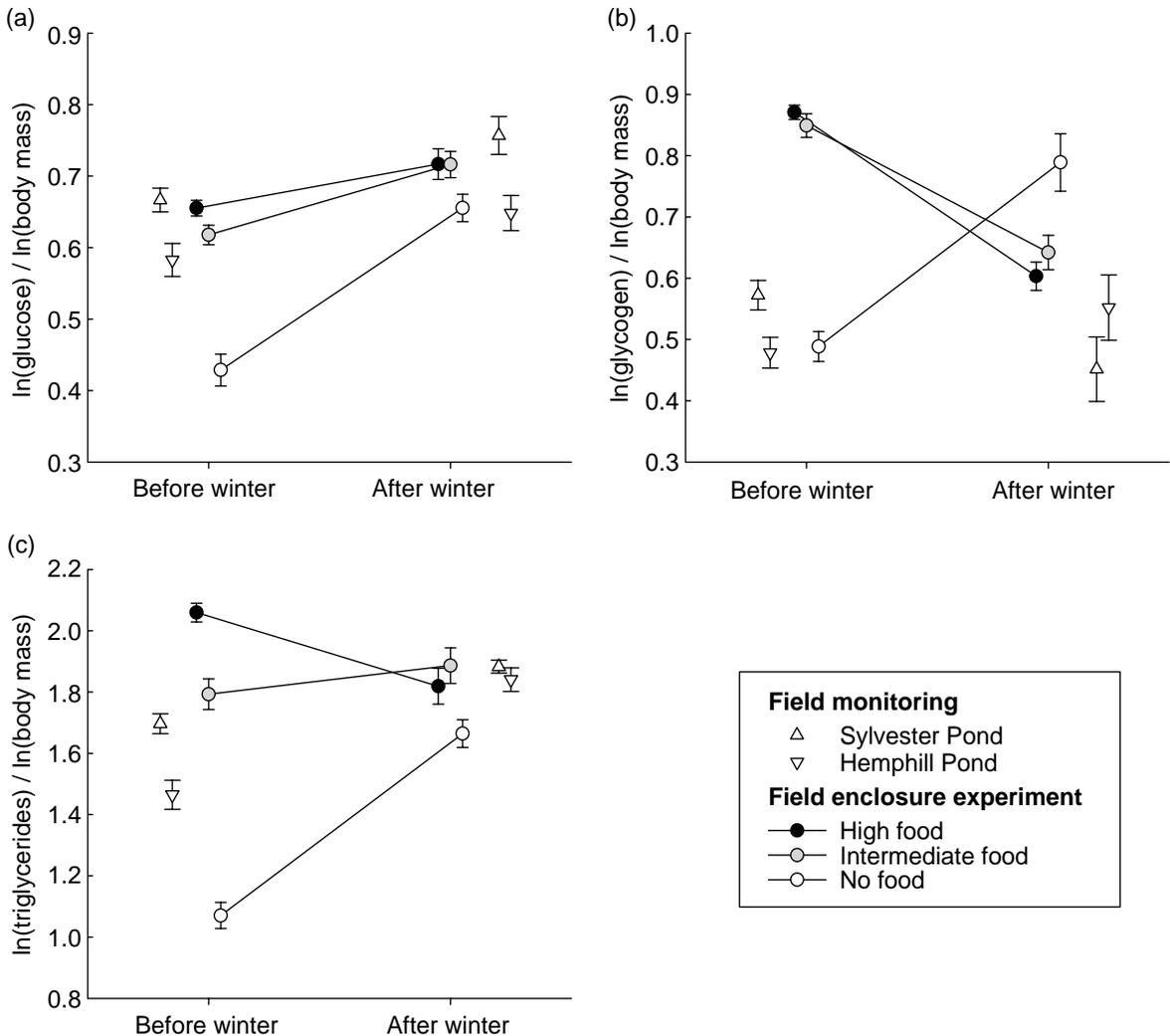

Fig. 2. Mass-corrected levels of (a) glucose, (b) glycogen, and (c) triglycerides of *Lestes eurinus* larvae as a function of food manipulation before and after winter. Ln-transformed means ± 1 SE are presented of values originally measured as µg mg^{-1} dry mass. The connected symbols represent means of larvae from the field enclosure experiment in Sylvester Pond. The non-connected symbols represent means of unmanipulated larvae from the field monitoring.

Fig. 2b). This resulted in similar glycogen levels after winter for larvae of both populations (Tukey test, p = 0.93). Levels of triglycerides increased during winter, especially in larvae from Hemphill Pond (ANCOVA, population × timing, $F_{1/55} = 5.31$, $p < 0.05$; Fig. 2c). As a result, after winter the levels of triglycerides were the same in both populations (Tukey test, p = 0.84).

Enclosure experiment

During the winter enclosure experiment, water temperature was on average 4.2°C (range: 2.53 – 6.76°C). Temperature for the first time rose above 5°C three days before the ice receded and the experiment was stopped. Winter survival was high (no food: 86%, intermediate food: 83% and high food: 92%) and did not differ among the food treatments (loglinear analysis, food × survival: $\chi^2_2 = 1.07$, p = 0.59). The initial mass of the larvae that died (22.62 ± 1.77 mg [mean ± 1 SE]) did not differ from the initial mass of the larvae that survived (21.78 ± 0.66 mg) ($t_{107} = -0.45$, p = 0.65).

After the food manipulation, mass decreased going from the high food (23.2 ± 1.0 mg [mean ± 1 SE]), over the intermediate food (21.4 ± 1.1 mg) to the no food treatment (20.7 ± 1.2 mg) (ANOVA on log-transformed data, linear contrast, $F_{1/89} = 3.01$, $p_{one-sided} < 0.05$). Growth rates during the winter were very low, and higher for larvae that were previously exposed to the no food treatment than for larvae of the intermediate food treatment and the high food treatment (ANOVA, food: $F_{2/92} = 5.47$, $p < 0.01$; Fig. 1b). Growth rates were significantly higher than zero for the no food treatment (one-sample t-test, $t_{31} = 4.90$, $p < 0.0001$) and the intermediate food treatment ($t_{29} = 2.77$, $p < 0.01$), but not for the high food treatment ($t_{32} = 0.90$, $p = 0.38$). As a result, masses were not different among the food treatment levels after winter (high food: 23.4 ± 1.0 mg, intermediate food: 21.9 ± 1.2 mg and no food: 21.6 ± 1.3 mg) (ANOVA on log-transformed data, linear contrast, $F_{1/89} = 1.47$, $p_{one-sided} = 0.12$).

Mass-corrected energy reserve levels changed during winter and this change depended on the preceding food treatment (MANCOVA, food: $F_{6/162} = 22.08$, $p < 0.0001$; timing: $F_{3/81} = 36.19$, $p < 0.0001$; food × timing: $F_{6/162} = 21.70$, $p < 0.0001$). Before winter (directly after the food manipulation), levels of the three energy reserve pools were lower in larvae of the no food treatment compared to larvae of the intermediate and high food treatments (Tukey test, all $p < 0.001$) which did not differ among each other (all $p > 0.13$; Fig. 2). During winter, levels of glucose increased, especially in larvae of the no food treatment (ANCOVA, food × timing: $F_{2/83} = 11.25$, $p < 0.0001$;

Fig. 2a). This resulted in similar glucose levels for larvae of all food treatments after winter (Tukey test, all $p > 0.06$). Levels of glycogen decreased during winter for larvae of the intermediate and high food treatments, but strongly increased for larvae of the no food treatment (ANCOVA, food × timing: $F_{2/83} = 81.50$, $p < 0.0001$; Fig. 2b). This resulted in higher glycogen levels after winter for larvae of the no food treatment compared to larvae of the other two food treatments (Tukey test, both $p < 0.001$). Levels of triglycerides did not change during winter in larvae of the intermediate and high food treatments, but strongly increased in larvae of the no food treatment (ANCOVA, food × timing: $F_{2/83} = 36.39$, $p < 0.0001$; Fig. 2c). This resulted in similar triglyceride levels for larvae of all food treatments after winter (Tukey test, all $p > 0.08$).

Discussion

Our results show that larvae of the damselfly *L. eurinus* continued to grow, albeit very slowly, under the prolonged period of ice cover on New England ponds. Moreover, our data indicate compensatory growth both in terms of mass and energy reserves. Note that the observed growth patterns in the field enclosure experiment cannot be attributed simply to size-selective mortality where larvae with the lowest mass and energy reserves would have been eliminated (Munch et al. 2003, but see Byström et al. 2006). First, as shown in the results, survival was very high (32 out of 37 larvae survived in the no food treatment where the compensatory response occurred), moreover it was not different among food treatments. Second, mortality was random as, except for one animal, larvae died because of handling effects when taking the enclosures out of the pond. In line with this, the initial mass of the larvae that died did not differ from the initial mass of the larvae that survived. Although we have no actual data to support this, there is no reason to assume that mortality due to winter conditions during the field monitoring, was not similarly random with regard to phenotype. Under these unmanipulated field conditions, an additional selection agent may, however, have been predation. Yet, the top predators in the permanent fishless lakes inhabited by *L. eurinus* are large dragonfly larvae (Stoks and McPeek 2003, 2006), which impose no size-selective mortality on *Lestes* larvae (Stoks et al. 1999).

Overall, positive growth rates in terms of mass during winter were found under natural field conditions and in the field enclosure experiment. Growth during winter has been demonstrated in many insect orders, including Diptera, Ephemeroptera, Plecoptera and Trichoptera (overview in Danks 1991). However, to our knowledge, no studies have reported compensatory growth in mass during winter in an invertebrate. In our

study, growth rate patterns for body mass during winter were consistent with a pattern of compensatory growth. In the field enclosure experiment, significant positive growth rates were observed in larvae previously kept at the no food and the intermediate food treatments but not in larvae from the high food treatment. Also the field monitoring data may suggest compensatory growth in terms of mass. Growth rates in autumn and associated masses just before winter were higher in Sylvester Pond than in Hemphill Pond, and in accordance with a compensation scenario, positive winter growth was present in larvae in Hemphill Pond, but not in Sylvester Pond.

As expected, larvae also showed compensation in energy reserves. Although larvae in the no food treatment started winter with lower levels of all energy stores, after winter they had reached similar (glucose and triglycerides) or even higher (glycogen) energy stores than the other food treatment groups. This suggests that larvae of the no food treatment had a higher food intake during winter which may also explain why they were the only food treatment group to increase glycogen and triglyceride levels during winter. While levels of glycogen increased sharply over winter in larvae of the no food treatment, they decreased somewhat in larvae of the two other food treatments. Glycogen can easily be converted in glucose when the reserves need to be mobilized (Klowden 2002), and our data suggest that larvae of the latter treatments had to partly deplete their glycogen stores to maintain glucose levels, while larvae of the no food treatment could probably rely on their higher food intake to achieve this.

Also the data of the field monitoring are consistent with a pattern of compensatory growth in energy reserves. Although larvae from Hemphill Pond started winter with lower levels of all energy stores, after winter they had similar levels of glycogen and triglycerides to larvae in Sylvester Pond. That all energy stores increased during winter in larvae from Hemphill Pond, and less so (triglycerides) or even not (glycogen) in larvae from Sylvester Pond suggests they had a higher food intake. The assumed lower food intake in larvae from Sylvester Pond may have forced them to partly deplete glycogen levels and convert them into glucose whose levels slightly increased during winter. The reason for the apparent difference in intake is unknown.

As far as we know, this is the first demonstration of compensatory growth in energy reserves under winter field conditions. So far, experimental proof of compensatory growth in energy reserves under winter conditions had been given only in fish, but not under natural field conditions (Metcalfe and Thorpe 1992, Bull and Metcalfe 1997). Alvarez and Nicieza (2005) did report compensatory growth in terms of mass during winter in the field in brown trout. They pre-

manipulated fish in the laboratory by giving half of them a starvation treatment before releasing them in a river. As in our study, brown trout had no differential winter survival, and showed compensatory growth in terms of mass during winter at mean temperatures of $9.4°C$ (range: $7.8 - 11.2°C$). Because energy reserves were not directly measured in their winter experiment, no conclusions can be drawn about any compensatory growth in energy reserves (Forsman and Lindell 1991).

It is intriguing why not all larvae showed the higher increase in body mass and energy reserves. Actually, larvae that already showed relative high energy levels before winter (larvae from Sylvester Pond in the monitoring study, high food treatment larvae in the enclosure experiment) did not have a growth rate that significantly differed from zero during winter. This is a common strategy in hibernating animals (Mrosovsky and Sherry 1980). Only when animals under winter conditions are confronted with an energy deficit before winter, they do feed and grow during winter (Metcalfe and Thorpe 1992). This suggests that costs exist. Costs of compensatory growth are still poorly understood (Metcalfe and Monaghan 2001). Recent studies showed costs after a period of compensatory growth in terms of a reduced starvation resistance, lower investments in immune response and in energy reserves in the long-term (Morgan and Metcalfe 2001, Stoks et al. 2006a, 2006b), and an increased winter mortality (Johnsson and Bohlin 2006, but see Johnsson and Bohlin 2005). We could not detect a cost in winter survival associated with compensatory growth in the enclosure experiment. However, winter mortality by predation may be one cost involved. In a field enclosure experiment during winter in the presence of predators we could demonstrate that during winter larvae not only showed positive growth rates but also experienced significant mortality by predation (De Block unpubl.). Faster growing larvae of another *Lestes* species have been shown to be more vulnerable to predation (Stoks et al. 2005b), and compensatory growth was not affected by the presence of predators in another damselfly (Dmitriew and Rowe 2005). However, the observed mortality rate by *Anax* predation on *L. eurinus* during winter $(0.00417 \pm 0.00053 \text{ d}^{-1}$ [mean ± 1 SE]; De Block unpubl.) was about eight times lower than the one observed for this species in a similar field enclosure experiment during autumn $(0.036 \pm 0.003 \text{ d}^{-1}$ [mean ± 1 SE]; Stoks and McPeek 2003). So whether mortality by predation during winter is strong enough to cause a cost for compensatory growth is a conjecture that waits experimental testing.

Whatever the costs, we hypothesize that the ability to compensate energy reserves during winter may have important ecological ramifications. It alleviates the necessity of accumulating enough energy reserves before winter to survive winter and, as such, it would reduce

the time constraints imposed on animals to rapidly accumulate energy reserves before the onset of winter (Rowe and Ludwig 1991). Several other selective pressures, like mortality by predation, are operating in autumn and may preclude animals to reach the necessary energy reserves at the start of winter (Stoks et al. 2005a). Compensatory growth during winter may potentially allow animals to prioritize these other selective pressures in autumn, especially since pressures like mortality by predation are likely less intense during winter conditions (see above). Even for animals with an energy deficit that survived the winter, energy levels after winter may be too low for maturation. Therefore, as in autumn, compensatory growth during winter may potentially also partly alleviate the need for costly compensatory growth in spring. To test these conjectures, and to fully understand the impact of compensatory growth in energy reserves during winter we need studies that not only manipulate energy reserves before winter but that also manipulate the ability to compensate during winter, as well as studies comparing related taxa that differ in their capacity for winter compensatory growth. Such studies will shed light on its potential importance in shaping life history decisions in autumn and in spring. We hypothesize that in species showing compensatory growth in energy reserves, resource availability during winter might be as or more important than energy reserves before winter.

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