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SHORT COMMUNICATION

Metabolic rate in the signal crayfish (Pacifastacus leniusculus) is temporally consistent and elevated at molting

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Although the temporal consistency of resting metabolic rate in individual animals is generally considered to be a universal phenomenon, studies on invertebrates are still scarce. Here, we studied the repeatability of standard metabolic rate in the signal crayfish (Pacifastacus leniusculus). We measured oxygen consumption twice on the same individuals, on average in 97-day intervals. At intermolt stage, the standard metabolic rate was a repeatable trait. However, molting increased significantly the minimum metabolic rate, thus emphasizing the role of animal physiological state in determining the rate of metabolism.

Keywords: signal crayfish; Pacifastacus leniusculus; oxygen consumption; resting metabolic rate; molting; consistency

Standard or resting metabolic rate is the minimum metabolic rate of an unfed animal required for maintaining the basic physiological functions (Jobling 1994). Maintenance costs of individual animals are highly variable, and existence of two- to threefold differences in minimum metabolic rate of conspecifics is not uncommon (Careau et al. 2008; Burton et al. 2011). According to the present view, consistent individual differences in resting metabolic rate are somewhat ubiquitous (Nespolo & Franco 2007; Biro & Stamps 2010; Burton et al. 2011). However, studies in invertebrates are still very rare and in crustaceans, for example, only one previous study exists. Alcaraz and Kruesi (2012) reported that standard metabolic rate was temporally consistent in the hermit crab (Calcinus californiensis). In the noble crayfish (Austacus astacus), temporally consistent patterns have also been found in behavior (Vainikka et al. 2011) suggesting possible consistency in metabolism as well. However, since the consistency of metabolic rate may temporarily disappear, e.g. under unfavorable conditions (O’Connor et al. 2000; Careau et al. 2008; Alcaraz & Kruesi 2012) or due to life-history transitions (Seppänen et al. 2010), it is important to carry out long-term individual-level studies.

Crayfish and other decapod crustaceans are characterized by intermittent growth and regular molt cycle due to their heavily calcified exoskeleton. For growth to occur, crayfish have to periodically replace the exoskeleton by expelling the old one and hardening the new one that is expanded by water absorption (Chen & Watson 2010). This process is known as molting, and it includes various physiological, biochemical, morphological
and behavioral changes (e.g. Chang 1995). Molting is under hormonal control and due to its high metabolic demands it is also energetically costly (Penkoff & Thurberg 1982; Cockcroft & Wooldridge 1985).

The aim of the present study was to explore the temporal consistency of the resting metabolic rate of signal crayfish (Pacifastacus leniusculus) undergoing a molting cycle. We conducted two respirometry trials for the same individuals and, on the basis of earlier studies with different taxa, we predicted that resting metabolic rate is a repeatable trait (Nespolo & Franco 2007) and it increases at the time of molting (Penkoff & Thurberg 1982). The time period between the trials was over three months and the majority of the individuals molted during the course of the study.

In November 2010, mature male signal crayfish were obtained from semi-natural ponds at the Finnish Game and Fisheries Research Institute’s (FGFRI) Evo research station. The crayfish originated from Laukaa hatchery of the FGFRI had been brought to the Evo ponds as one-summer-old individuals. Only males in good physical condition with intact and approximately similar-sized chelipeds as well as healthy mouthparts were chosen for the experiments. Upon arrival in the laboratory, the crayfish were individually numbered using a white marker pen (Textmark 250) and then moved to individual compartments, measuring 11 cm (width) × 14.5 cm (length) × 11 cm (water depth). The compartments were built in 56 × 75 cm tanks, which were equipped with a water flow-through system. The individuals in a tank were physically, but not chemically, separated from each other. Crayfish were fed ad libitum with carrot and periodically also grain of rice. The photoperiod (12L:12D) and water temperature (12.5 ± 1.0 °C) were kept constant.

Oxygen consumption of the crayfish was measured at 12.5 °C by an automated three-chamber intermittent-flow respirometer equipped with YSI 5750 polarographic oxygen sensor (Forstner 1983; Voutilainen et al. 2011). The respirometer system included three parallel acrylic chambers (volumes 158–167 mL), and a single crayfish was placed in each chamber during a trial. The flow rate was about 200 mL min⁻¹. Before measurements the crayfish were deprived of food for 24 h. Each measurement lasted for 24 h (photoperiod 12L:12D). During this period, the oxygen consumption of each chamber was recorded for 15 min every hour and average rate of this time was extrapolated to an hourly value. The signals from the polarographic oxygen sensor were fed online into the computer and integrated each minute. The oxygen electrode chamber and the animal chambers were flushed after each measurement with fully oxygen-saturated water. Microbial oxygen consumption of the respirometer was measured at the beginning and end of the trial and it was subtracted from the total decline of oxygen. After the measurements the crayfish were weighed for the fresh mass. Mass-specific standard metabolic rate (μmol O₂ g⁻¹ h⁻¹) was defined as the lowest oxygen consumption value recorded (for 15 min) during the trial. Crayfish size range was from 12.6 to 37.7 g (22.0 ± 7.3 g, mean ± SD). However, the mass-specific metabolic rate was not dependent on the body mass of the animals (linear regression, \( r^2 = 0.016, p = 0.409 \)).

Oxygen consumption of the same individually marked crayfish was measured twice: first in October/November 2011 and for a second time in January/February 2012. There were originally 45 crayfish of which 10 individuals died between the first and second trials. The average time between the two trials was 97 days (range 76–112 days). Our preliminary expectation was that, as a sheltering species, signal crayfish would spend long periods inactive in small respirometer chambers, and it would be easy to record a minimum metabolic rate that corresponds to the standard metabolic rate of each
individual. The first trial, however, gave indications that this was not the case because metabolic rates of certain individuals stayed at high level throughout the measurement period. Hence, a video recording (Logitech Webcam 9000 Pro) was applied in the second trial to ensure that the minimum metabolic rate corresponds to a period with no locomotor activity of the crayfish. Dim red light illumination was used in the night-time recording.

Due to the long duration of the study, crayfish were molting before and during the oxygen consumption measuring period. Hence, measurements included intermolt, premolt and postmolt individuals. However, no soft-bodied molting crayfish were measured to avoid handling during this sensitive period. In the first trial, 13 individuals were measured prior to molting (8–79 days before molt) and 22 individuals after molting (8–61 days after molt). The remaining 10 crayfish did not molt at all during the study period. In Finland, the signal crayfish has two major periods of molting; one between late June and July and another one between late August and September (Westman & Savolainen 2002). The reason for an atypical molting cycle in our experimental crayfish was probably cool rearing temperature which retarded growth and, thus, delayed molting to late autumn and winter.

The range of standard metabolic rate i.e. the minimum oxygen consumption value of individual signal crayfish varied from 0.42 to 1.79 μmol O₂ g⁻¹ h⁻¹ in the first trial and from 0.38 to 0.93 μmol O₂ g⁻¹ h⁻¹ in the second trial. The video recording during the second trial indicated that minimum metabolic rates lower than 0.8 μmol O₂ g⁻¹ h⁻¹ represented rates with no or negligible (e.g. occasional movement of a single leg) spontaneous activity whereas rates exceeding 0.8 μmol O₂ g⁻¹ h⁻¹ included moderate or high levels of activity. Hence, the rates higher than 0.8 μmol O₂ g⁻¹ h⁻¹ could not be considered to represent standard metabolic rate and they were discarded from the later analyses. Using this criterion, a significant positive intraclass correlation (Lessells & Boag 1987) was found between the standard metabolic rate of individual crayfish in the first and second trial (r = 0.674, p = 0.002, n = 14; Figure 1). This demonstrates that standard metabolic rate of signal crayfish is a repeatable trait over a period of approximately three months. All these individuals were at the intermolt stage (at least 19 days from molting). On the other hand, molting significantly affected the minimum metabolic rate of signal crayfish so that it increased towards the molting date, reached its maximum a

![Figure 1](image-url)
few days prior to molting and decreased thereafter (Figure 2). Increased oxygen consumption rate before and during molting is a result of a set of physiological and biochemical changes, especially in the hepatopancreas and hemolymph of the crustaceans (Chang 1995; Galindo et al. 2009). In the present study, minimum metabolic rate was over twofold in animals within 10 days of molting compared with those measured at another times (Figure 2), and the difference was statistically highly significant ($t$-test, $t = 7.576$, $p < 0.001$). The locomotor activity may also play a role here because activity was not monitored in the pre- and post-molt individuals. However, this is unlikely since decapod crustaceans generally decrease their activity as molting approaches (Morgan 1978; Lipcius & Herrnkind 1982).

To conclude, our study provides evidence for long-term temporal consistency of the standard metabolic rate as well as molting-induced increase in minimum metabolic rate in a decapod crustacean. These findings are in line with earlier studies on the temporal repeatability of metabolic rate but also emphasize the significance of animal physiological state in determining the metabolic rate.

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