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## Preliminary observations on the effect of light and temperature on the hatching success and rate of *Lepidurus arcticus* eggs

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Dormancy, which arrests development, is a well-known survival strategy among animals living in the Arctic to overcome harsh periods. It is not clear if the dormant state in notostracans is controlled endogenously (diapause) or exogenously (quiescence). For *Lepidurus arcticus*, it is unknown how it responds to the photoperiod entrainment, if it has a biological clock and if it has a rhythmic expression of the clock genes. We studied the hatching success of resting eggs at four constant temperatures (5, 10, 15 and 25 °C) and under different illumination regimes [continuous light (LL) and continuous dark (DD)]. It was assumed that light and temperature are both important triggers, with temperature having the most pronounced effect. In our experiment, hatching occurred only at 5 and 10 °C, while we did not observe hatching at 15 and 25 °C. The highest percentage of eggs hatched was at 10 °C in LL (60%); the lowest was at 5 °C in DD (18%). The percentages hatched at 5 °C in LL (24%) and at 10 °C in DD (26%) were similar. Our results indicate that both temperature and light had a significant and interacting effect on hatching in *L. arcticus*, with temperature being the dominant factor controlling the process. This suggests that changes in temperature affecting the Arctic may significantly impact phenology of this key species in the region. Given that no hatching was observed at 15 °C or above, the persistence of this species may be at risk in areas where arctic lakes are expected to warm to such levels during the summer months.

KEY WORDS: biological rhythms, dormancy, hatching, Notostraca, Arctic.

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## INTRODUCTION

*Lepidurus arcticus* (Pallas 1793) is a notostracan crustacean with a circumpolar distribution in the northern hemisphere where it inhabits freshwater ponds and lakes (Rogers 2001). It is especially abundant where the sediment surface consists of soft organic material and in vegetated patches. The animals live and eat mainly in the benthic environment but may also move actively around in the water column (Christoffersen 2001; Calizza et al. 2016; Mancinelli & Pasquali 2016). The species life cycle has been described in some detail by Borgström and Larsson (1974) and Wojtasik and Bryłka-Wołk (2010). In brief, *L. arcticus* eggs hatch when the pond in which they have overwintered thaws and water temperature is a few degrees above freezing. The larval stage, initially approx. 2 mm long, moves through five juvenile instars before the adult stage is reached. This process takes 1–2 months depending on temperature and food availability (V. Pasquali pers. observations). The observed size of adult specimens ranges between 1.5 and 2.5 cm in length, with specimens of 3 cm in length or more seldom observed. In Svalbard, adult specimens are commonly observed in August, when females lay eggs in littoral zones before dying.

Together with Anostraca, Notostraca represent a good example of species producing resting eggs, which can remain in a dormant state for a long period until favourable conditions occur. During dormancy, the development is arrested in order to cope with periods of unfavourable environmental conditions. In general, “quiescence” and “diapause” are considered two forms of dormancy but with different physiological bases. Quiescence is imposed from external conditions (exogenously controlled), while diapause it is controlled from internal factors (endogenously controlled) (Cáceres 1997; Radzikowski 2013). Diapause in arthropods is a useful mechanism for programming annual changes in the behaviour and physiology of organisms; diapause depends on the timing of biological mechanisms to control its initiation and termination. One means to time diapause is photoperiodism. By measuring the length of the daily light period, photoperiodic species can initiate specific functions at the optimal time of the year. In some species, such as *Drosophila melanogaster*, photoperiod and temperature may jointly regulate timing of diapause (Saunders 1990), while in other species annual adaptive changes may also depend on an internal sense of calendar time, a so-called circannual clock (Hazlerigg & Lincoln 2011).

Circannual processes may be particularly important for exiting from diapause, since optimal timing for emergence from the resting state may anticipate favourable environmental conditions (Cáceres 1997; Radzikowski 2013). Presently, there are few data about the various environmental parameters affecting hatching of diapausing cysts in large branchiopods such as *Lepidurus*. In many notostracan and anostracan species hatching is influenced by light, temperature, pH and salinity (for a review see Brendonck 1996; Schönbrunner & Eder 2006), as well as by some biotic parameters: nutrients, predators, population density (Mitchell 1990; Spencer & Blaustein 2001). The dominance of one factor over the others necessarily determines the magnitude of change in environmental conditions that may or may not affect the timing of hatching in natural populations. Presently, it is not clear if the dormant state in Notostraca is controlled endogenously (diapause) or exogenously (quiescence), while it seems that both mechanisms may play an important role in other branchiopods (Brendonck 1996; Fryer 1996). To clarify the dominance of internal or external factors may be crucial for understanding adaptation in the Arctic Notostraca *Lepidurus arcticus*. Indeed, while the region is characterized by extremely marked seasonality in photoperiod, it also

represents one of the areas most impacted by climate change in terms of increasing temperature during recent decades (IPCC 2013).

The study of *L. arcticus*, as other polar species (Pasquali 2015; Pasquali et al. 2016, 2017) or cave-dwelling species (Pasquali & Sbordoni 2014), is particularly interesting for chrono-biological studies because it is commonly present at high latitudes, where particularly marked photoperiodic variations are naturally observed. However, only few authors have studied the hatching process of this species under controlled conditions. Borgstrøm and Larsson (1974) collected adults of *L. arcticus* in Norway during August 1972 and kept the animals under natural conditions until egg-laying. Eggs were kept at 4–5 °C for 5 months in the original pond water, but no information on photoperiod condition was provided. During February 1973, 15 of the eggs hatched, but they died as first instar nauplii. The remaining eggs were then kept at room temperature and five more eggs hatched during late February and early March. Only few individuals developed but only one reached the third instar stage. Likewise, Fryer (1988) reported that *L. arcticus* eggs could hatch without a previous drying or freezing period. He kept eggs attached to moss fronds at ca 4 °C and dimly illuminated for several hours a day mimicking environmental conditions experienced during dormancy. The eggs began to hatch when brought to room temperature and Fryer (1988) hypothesized that hatching is initiated by osmotic swelling of a fluid-filled capsule bounded by the inner of two thin, transparent membranes that enclose the larvae. A process that would imply that emergence is a passive response to changes in environmental temperature. However, it is not known if *L. arcticus* responds to the changes in photoperiod entrainment, increase in ambient temperatures or if it has a biological clock that ensures a timely hatching. Knowledge on the physiological regulatory mechanisms can be useful for understanding the biological rhythms and phenology of arctic species in general and for an aquatic invertebrate as *L. arcticus* because of ongoing climate changes (Walther et al. 2002; Love et al. 2010). Here, we tested the effect of light and temperature, and their interaction, on the hatching of *L. arcticus* eggs from a shallow lake in Svalbard under controlled laboratory conditions.

## MATERIALS AND METHODS

The experiment was performed on eggs of *Lepidurus arcticus* collected in Solvatnet (78°56'N, 11°57'E), a small shallow (< 1 m) pond located in Ny-Ålesund (78°55'N, 11°56'E) on the Brøggerhalvøya peninsula on the west coast of the Spitsbergen archipelago (see Mancinelli & Pasquali 2016, for further details and Fig. 1 for the annual temperature cycle; Mazzola et al. 2016). On 27 May 2015 the pond surface was still totally frozen with an overlying ice of approx. 50 cm and no open water was observed, while on June 3rd the ice began to crack and it was possible to access the sediment surface of the pond (Table 1). The bottom water temperature was 0.6 °C. *Zignema* sp. algae mats with *L. arcticus* eggs were hand-picked and immediately transferred to the laboratory in 10 L containers filled with water from the pond.

A total of 400 eggs were manually separated by tweezers from the algae mats and incubated inside a Gram Bioplus 500 ER (–2/+20 °C) and Thermo Scientific Heratherm (+17/+40 °C) in groups of 50 eggs (randomly picked from the entire batch) in 250 mL glass beakers with 200 mL unfiltered pond water at four constant temperatures: 5, 10, 15, and 25 °C ( $\pm 0.5$  °C) and at two photoperiods: continuous light (LL) and continuous darkness (DD). Light levels in the experimental incubator were monitored with HOBO Light data loggers. In LL the light level was 1000 lumens/m<sup>2</sup>, while in DD light level it was 0 lumens/m<sup>2</sup>. Experimental incubation started on June 3rd and lasted 26 days, during which beakers were monitored every 12 hr. During this period, samples of algal mat were monitored daily in order to observe eventual hatching in natural conditions.

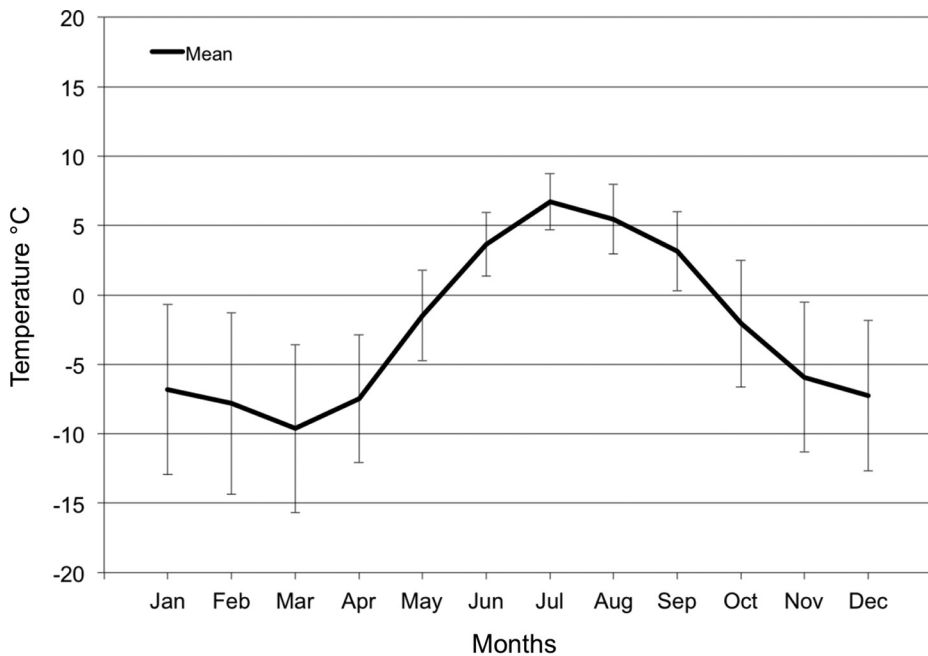


Fig. 1. — Average annual air temperature in Ny-Ålesund from 2010 to 2017. Data are presented as mean  $\pm$  SD. Data from Italian Arctic Data Center, Amundsen-Nobile Climate Change Tower, Consiglio Nazionale delle Ricerche (Mazzola et al. 2016).

The two temperature treatments of 5 and 10 °C, and LL photoperiod were established to mimic the conditions typically found in Arctic ponds where *L. arcticus* eggs normally hatch. In parallel, the DD photoperiod was chosen to mimic natural winter conditions in which darkness is known to maintain the eggs in a dormancy stage (Fryer 1988). The 15 °C condition was used as it mimics the near future expected temperature in the high-Arctic lakes and ponds, and 25 °C is the temperature at which cogeneric species within the genus *Lepidurus* have been found (Hann & Lonsberry 1991; Kuller & Gasith 1996).

Dim red light of  $\lambda > 650$  nm was used when working in DD conditions. Eggs were examined once a day to determine the rate of hatching, the nauplii were removed and counted. Temperature and photoperiod effects on hatching success (observed vs expected) were examined by Chi-square tests.

## RESULTS

Data on hatching can be found in Table 2. *L. arcticus* hatched at 5 and 10 °C in LL and DD, respectively. No eggs hatched at 15 and 25 °C, under either of the photoperiods.

### *Hatching success*

It was observed that out of the 200 remaining eggs (i.e., 5 and 10 °C treatments), 64 hatched (Table 2), corresponding to an overall 32% hatching success. Hatching began after 7 days of incubation (which timewise corresponded to the middle of June).

Table 1.  
Observations on the state of Solvatnet during the summer 2015.

Date	Water temperature	Observations
27 May	not measured	Lake surface totally frozen (= 100% coverage); ice reaching the lake bottom
03 June	+ 0.6 °C	Ice surface broken with < 10 cm wide cracks, access to the frozen sediment surface
08 June	+ 1.2 °C	Defrosting of surface ice starting, bottom sediment still frozen
10 June	+ 1.6 °C	Defrosting of surface ice ongoing, bottom sediment still frozen
14 June	+ 2.4 °C	Surface partially (ca 60%) free from ice, bottom sediment partially thawed
25 June	+ 9.7 °C	Surface ice and sediment totally thawed, presence of <i>L. arcticus</i> nauplii
06 July	not measured	Some <i>L. arcticus</i> with dark coloured skin on the back observed
08 July	+ 11 °C	More and bigger <i>L. arcticus</i> observed (5–8 mm)
19 July	+ 11.5 °C	Multiple <i>L. arcticus</i> of various sizes observed (8–10 mm)
30 July	not measured	Only <i>L. arcticus</i> larger than 10 mm observed
02 September	+ 2.0 °C	Few <i>L. arcticus</i> present but not alive (observed as motionless on top of the algae mats)

Table 2.

Number (No.), percentage (%) and hatching rates of *Lepidurus arcticus* eggs in continuous light (LL) and continuous dark (DD) conditions, at different temperatures (T). Fifty eggs were used in each experiment. Hatching rate was calculated as the number of hatched eggs at a given time divided by the difference between the time of last and first hatching, measured in days.

T (°C)	LL			DD		
	No. hatched	% hatched	Rate	No. hatched	% hatched	Rate
5	12	24	1.1	9	18	1
10	30	60	4.3	13	26	2.2
15	0	0	–	0	0	–
25	0	0	–	0	0	–

A majority of the eggs (67%) were hatched at 10 °C, while the remaining fraction (33%) hatched at 5 °C. This difference was significant (Chi-square = 7.56,  $P < 0.01$ ). With respect to photoperiod, there was a significant difference between LL, where 66% hatched, and DD where 34% hatched (Chi-square = 6.25,  $P < 0.05$ ). There was, however, no significant interactions of the combined temperature and photoperiod on hatching at 5 °C as we observed 57% of the eggs hatching in LL and 43% in DD (Chi-square = 0.42,  $P < 0.05$ ). This turned out to be different for the eggs incubated at 10 °C as we found a significant higher fraction (70%) hatching in LL compared to 30% in DD (Chi-square = 6.72,  $P < 0.01$ ).

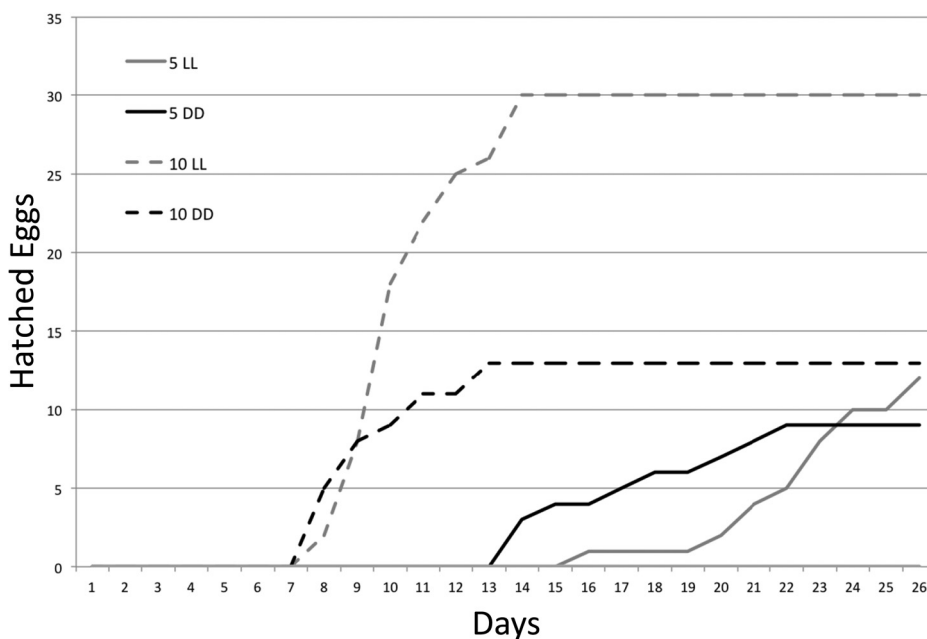


Fig. 2. — Cumulative number of hatched eggs in continuous light (LL) and continuous darkness (DD) at different temperatures (i.e. 5 and 10 °C) during 26 days of experiment.

### Hatching rate

The hatching rate (determined as the number of hatched eggs at a given time divided by the difference between the time of last and first hatching, measured in days) showed significant differences between the tested groups (Chi-square = 4.0,  $P < 0.05$ ) (Table 2 and Fig. 2). The highest hatching rate of 4.3 eggs/day was observed at 10 °C and under LL conditions, followed by 2.2 eggs/day at 10 °C in DD. A lower hatching rate was observed at 5 °C, both in LL (rate = 1.1 eggs/day) and DD (rate = 1.0 eggs/day) condition.

### Nauplii appearance time

In general the time before an egg hatched appeared to be inversely related to the temperature. The first hatching was observed after 7 days at 10 °C both in LL and DD conditions, corresponding to June 10th, while at 5 °C it was observed after 13 and 15 days in DD and LL condition respectively (mean 14 days, corresponding to June 17th).

## DISCUSSION

Our experiments show that temperature and photoperiod in combination have an effect on the hatching of *Lepidurus arcticus*. Hatching occurred only at 5 and 10 °C, while no hatching at all was observed at 15 and 25 °C, most probably because these conditions exceeded the physiological tolerance for *Lepidurus* eggs. These findings on the effect of

temperature are in line with the observations reported by Borgstrøm and Larsson (1974) and Fryer (1988) on *L. arcticus* regarding the temperature as stimulus for starting the hatching, where 5 °C seemed to be the lowest threshold allowing the process.

Overall, we observed a higher hatching in continuous light than in continuous dark condition. Nevertheless, such difference was significant only when eggs were incubated at 10 °C. In our experiment the light-dark photoperiod was not applied, but it could have been an interesting condition to include to study the functioning of the biological clock. Light is known as a factor that induces hatching in branchiopods including Notostraca (Kashiyama et al. 2010), moreover *L. arcticus* in Svalbard is present only during the summer period with the continuous light condition. Also, for the photoperiod condition our data are in accordance with observations reported in the literature. Indirectly, Fryer (1988) observed that dark condition maintained the eggs in a dormancy stage. Another study demonstrated that the related species *Triop cancriformis* and *Lepidurus apus* (Kuller & Gasith 1996), likewise, have lower hatching success in darkness than in light (by up to one order of magnitude).

The power of our approach is a cross-analysis of all the conditions used in our experimental design: temperature from 5 to 25 °C, light conditions LL and DD, the hatching rate and the nauplii appearance time. For a more complete comprehension of the biological aspect of the hatching, the interaction between the applied experimental conditions should be considered. Indeed, temperature and light are the main triggers for controlling the dormant stage, and their interaction (a synergetic effect of temperature and light) could be considered a “third” factor affecting the process. Based on the results, we hypothesize that increased hours of light per day and increased temperature are both important factors for termination of dormancy and that the combined effect is stronger than each effect alone. Notably, the day of first hatching under controlled conditions (both for the continuous light and the continuous darkness treatment) occurred when lake temperature in Solvatnet was + 2 °C, but the lake bottom was still frozen and no nauplii were observed. The observed high rate of hatching at 10 °C is also in line with the data obtained by Lakka (2013) based on respiration rates and with the observations of Kuller and Gasith (1996) on *Lepidurus apus*. The hatching rate at 5 °C showed similar values between LL and DD, being roughly the half or less of that observed at 10 °C. Appearance time also showed a clear difference between 10 and 5 °C, but no significant difference between LL and DD were observed. We hypothesize, that the dominant effect of temperature on hatching process may be related to the specific environmental conditions under which our study species evolved. Indeed, hatching in *Lepidurus* naturally occurs during the summer season in Svalbard, when lake water temperature typically increases from 0 to 10 °C. In lake Solvatnet, such temperature is typically observed in August. This also coincides with 24 hr of sunlight, which starts to light the lake even before the ice melting. Hatching in such conditions allow specimens to appear in the lake during the productive season, when also primary production in the lake is boosted by temperature and light (Vincent et al. 2008). Thus, the limiting effect of 5 °C on hatching may comply with the important role of avoiding an excessively early hatching, which could result in a mismatch between appearance of nauplii and availability of trophic sources in Solvatnet.

While data allowing comparisons with populations inhabiting lakes characterized by lower temperatures are not available at present, future comparisons would clarify if temperature thresholds observed here and elsewhere (Borgstrøm & Larsson 1974; Fryer 1988) generally apply to *L. arcticus* or are influenced by the specific environmental conditions to which different populations are exposed.



From this study we can conclude that the “moment” (i.e. the beginning of the short Arctic summer season) and then the “conditions” (i.e. temperature and light) allow and control the hatching of *L. arcticus* eggs. Our results provide a clear evidence that quiescence mechanisms is significant for this species, given that hatching was observed in the lab when no appearance was observed in the lake from where eggs were collected. We believe that such discrepancy between laboratory and field observation supports the significant role of light and temperature (instead of endogenous circannual factors) on the hatching of this crustacean eggs. In turn, an open question remains on the concomitant role of diapause. Nevertheless, given that both quiescence and diapause seems to play an important role in other branchiopods (Brendonck 1996; Fryer 1996), and that hatching in *Lepidurus* populations in the Brøggerhalvoya peninsula occurs over a relatively restricted time-range (i.e. weeks) across lakes differing in temperature conditions, further investigation on this possibility seems worthy. In parallel, it could further be hypothesized that not only temperature, but also other environmental factors, such as water pH, could be involved in the process, likely interacting with the two factors considered here, as observed for *Triops cancriformis* (Schönbrunner & Eder 2006). In shallow Arctic lakes, the pH of the water changes when the snow begins to melt. This aspect certainly warrants further detailed investigations considering the interaction of multiple environmental factors on the process of hatching both under controlled conditions and in the field.

While preliminary, the significant effect of temperature on hatching in *L. arcticus* reported here both under light and dark conditions suggests that climate change, and specifically warming affecting the Arctic (IPCC 2013), will impact the biological cycle of this species. In turn, this may have implications for the food web that *L. arcticus* is part of (Christoffersen et al. 2008). Indeed, earlier hatching during May–June due to increased mean air and thus water temperature could imply a mismatch between the presence of *L. arcticus* in Arctic lakes and the abundance of its prey (e.g. *Daphnia* spp.) and predators (e.g. Arctic terns and other aquatic birds), thereby potentially decoupling food availability and demand across trophic levels (Christoffersen et al. 2008; Calizza et al. 2018), with subsequent potential bottom-up and top-down cascade effects at the ecosystem scale (Fazi & Rossi 2000; Mancinelli et al. 2007; Post et al. 2009; Calizza et al. 2013; Costantini et al. 2014; Mancinelli & Mulder 2015).

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#### DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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## REFERENCES

- Borgstrøm R, Larsson P. 1974. The three instars of *Lepidurus arcticus* (Pallas), (Crustacea: Notostraca). *Nor J Zool.* 22:45–52.
- Brendonck L. 1996. Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). *Hydrobiologia.* 320:85–97.
- Cáceres CE. 1997. Temporal variation, dormancy, and coexistence: a field test of the storage effect. *Proc Nat Acad Sci.* 94:9171–9175.
- Calizza E, Careddu G, Sporta Caputi S, Rossi L, Costantini ML. 2018. Time- and depth-wise trophic niche shift in Antarctic benthos. *PLoS ONE.* 13:e0194796.
- Calizza E, Costantini ML, Rossi D, Pasquali V, Careddu G, Rossi L. 2016. Stable isotopes and digital elevation models to study nutrient inputs in High-Arctic lakes. *Rend Lincei.* 27(Suppl. 1):191–199.
- Calizza E, Rossi L, Costantini ML. 2013. Predators and resources influence phosphorus transfer along an invertebrate food web through changes in prey behaviour. *PLoS ONE.* 8:e65186.
- Christoffersen K. 2001. Predation on *Daphnia pulex* by *Lepidurus arcticus*. *Hydrobiologia.* 442:223–229.
- Christoffersen KS, Amsinck SL, Landkildehus F, Lauridsen TL, Jeppesen E. 2008. Lake flora and fauna in relation to ice-melt, water temperature and chemistry at Zackenberg. In: H. Meltøfte, et al., editors. *High-Arctic ecosystem dynamics in a changing climate.* *Adv Ecol Res.* 40:371–389.
- Costantini ML, Calizza E, Rossi L. 2014. Stable isotope variation during fungal colonisation of leaf detritus in aquatic environments. *Fungal Ecol.* 11:154–163.
- Fazi S, Rossi L. 2000. Effects of macro-detritivores density on leaf detritus processing rate: a macrocosm experiment. *Hydrobiologia.* 435:127–134.
- Fryer G. 1988. Studies on the functional morphology and biology of the Notostraca (Crustacea: Branchiopoda). *Philos Trans R Soc B.* 321:27–124.
- Fryer G. 1996. Diapause, a potent force in the evolution of fresh-water crustaceans. *Hydrobiologia.* 320:1–14.
- Hann BJ, Lonsberry B. 1991. Influence of temperature on hatching of eggs of *Lepidurus couesii* (Crustacea, Notostraca). *Hydrobiologia.* 212:61–66.
- Hazlerigg DG, Lincoln GA. 2011. Hypothesis: cyclical histogenesis is the basis of circannual timing. *J Biol Rhythms.* 26:471–485.
- IPCC [Intergovernmental Panel on Climate Change]. 2013. *Climate change 2013: the physical science basis. Working group I. Contribution to the fifth assessment report of the inter-governmental panel on climate change.* Cambridge: Cambridge University Press.

- Kashiyama K, Ito C, Numata H, Goto SG. 2010. Spectral sensitivity of light-induced hatching and expression of genes mediating photoreception in eggs of the Asian tadpole shrimp *Triops granarius*. *Comp Biochem Physiol A*. 156(4):416–421.
- Kuller Z, Gasith A. 1996. Comparison of the hatching process of the tadpole shrimps *Triops cancriformis* and *Lepidurus apus lubbocki* (Notostraca) and its relation to their distribution in rain-pools in Israel. *Hydrobiologia*. 335:147–157.
- Lakka HK. 2013. The ecology of a freshwater crustacean: *Lepidurus arcticus* (Branchiopoda; Notostraca) in a High Arctic region [Master's Thesis]. Helsinki (Finland): University of Helsinki.
- Love OP, Gilchrist HG, Descamps S, Semeniuk CA, Bêty J. 2010. Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia*. 164:277–286.
- Mancinelli G, Costantini ML, Rossi L. 2007. Top-down control of reed detritus processing in a lake littoral zone: experimental evidence of a seasonal compensation between fish and invertebrate predation. *Int Rev Hydrobiol*. 92:117–134.
- Mancinelli G, Mulder C. 2015. Detrital dynamics and cascading effects on supporting ecosystem services. *Adv Ecol Res*. 53:97–160.
- Mancinelli G, Pasquali V. 2016. Body size-related constraints on the movement behaviour of the arctic notostracan *Lepidurus arcticus* (Pallas, 1973) under laboratory conditions. *Rend Lincei Sci Fisiche Naturali*. 27:207–215.
- Mazzola M, Viola AP, Lanconelli C, Vitale V. 2016. Atmospheric observations at the Amundsen-Nobile climate change tower in Ny-Ålesund, Svalbard. *Rend Lincei Sci Fisiche Naturali*. 27:7–18.
- Mitchell SA. 1990. Factors affecting the hatching of *Streptocephalus macrourus* (Crustacea; Eubranchiopoda) eggs. *Hydrobiologia*. 194:13–22.
- Pasquali V. 2015. Locomotor activity rhythms in high arctic freshwater crustacean: *Lepidurus arcticus* (Branchiopoda; Notostraca). *Biol Rhythm Res*. 46(3):453–458.
- Pasquali V, D'Alessandro G, Gualtieri R, Leccese F. 2017. A new data logger based on Raspberry-Pi for Arctic Notostraca locomotion investigations. *Measurement*. 110:249–256.
- Pasquali V, Gualtieri R, D'Alessandro G, Granberg M, Hazlerigg D, Cagnetti M, Leccese F. 2016. Monitoring and analyzing of circadian and ultradian locomotor activity based on Raspberry-Pi. *Electronics*. 5(3):58.
- Pasquali V, Sbordoni V. 2014. High variability in the expression of circadian rhythms in a cave beetle population. *Biol Rhythm Res*. 45(6):925–939.
- Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, Elberling B, Fox AD, Gilg O, Hik DS, Høye TT, et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science*. 325:1355–1358.
- Radzikowski J. 2013. Resistance of dormant stages of planktonic invertebrates to adverse environmental conditions. *J Plankton Res*. 35(4):707–723.
- Rogers DC. 2001. Revision of the nearctic *Lepidurus* (Notostraca). *J Crust Biol*. 21:991–1006.
- Saunders DS. 1990. The circadian basis of ovarian diapause regulation in *Drosophila melanogaster*: is the period gene causally involved in photoperiodic time measurement? *J Biol Rhythms*. 5:315–331.
- Schönbrunner IM, Eder E. 2006. pH-related hatching success of *Triops cancriformis* (Crustacea; Branchiopoda; Notostraca). *Hydrobiologia*. 563:515–520.
- Spencer M, Blaustein L. 2001. Hatching responses of temporary pool invertebrates in response to environmental signals. *Isr J Zool*. 47:397–418.
- Vincent WF, Hobbie JE, Laybourn-Parry J. 2008. Introduction to the limnology of high-latitude lakes and river ecosystems. In: Laybourn-Parry J, Vincent WF, editors. *Polar lakes and rivers: limnology of Arctic and Antarctic aquatic ecosystems*. Oxford: Oxford University Press; p. 1–24.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. *Nature*. 416:389.
- Wojtasik B, Brylika-Wołk M. 2010. Reproduction and genetic structure of a freshwater crustacean *Lepidurus arcticus* from Spitsbergen. *Pol Polar Res*. 31:33–44.