

A Novel Reproductive Response of a Planktonic Herbivore to Temperature Stress

Liza Pfaff 99, Joel Wickre 03 and Sierra Moldovan 02

Abstract

Global climate change, natural disasters and anthropogenic modifications of waterways may all lead to changing water temperature patterns in aquatic systems. We assessed the effects of different water temperatures on the reproductive rates of *Daphnia pulex*, a common primary consumer in aquatic ecosystems. Life table experiments were conducted using animals acclimatized to 10 °C and 20 °C water temperatures. Our findings at intermediate temperatures support findings from previous studies: *Daphnia* tend to show high reproductive rates at temperatures around 20 °C. (Bottrell, 1975; Lennon et al., 2001). We also observed unexpectedly high reproductive rates for 10 °C acclimatized clones in 30 °C treatments. These findings suggest the presence of a previously unrecognized coping mechanism present in this species for dealing with rapid, large temperature fluctuations.

INTRODUCTION

Recent global climate change models predict an increase in the frequency and duration of high temperature episodes (>35°C air temperature) as well as a decreased frequency but increased severity of storms across much of the northern temperate zone (Hansen *et al.*, 1988; Feddema & Mather, 1992, Moore *et al.*, 1997). Although the effects of these phenomena on aquatic systems are still largely unpredicted, certain types of systems will be more affected than others. For instance, shallow lake systems and systems with short water residence times will be subject to substantial temperature fluctuations. At present, natural disasters (e.g. volcanic eruptions) and anthropogenic disturbances (e.g. hypolimnetic water release from dams and thermal pollution) are able to bring about considerable changes in the water temperature of aquatic systems.

Daphnia are common planktonic grazers that provide an important link from primary producers to secondary consumers in aquatic food webs and will face many adaptive pressures as aquatic ecosystems are altered by climate change and disturbance (Chen & Folt, 1996). Members of this genus are found in many lake ecosystems throughout the world. Should *Daphnia* populations be disrupted, further alterations in algal and fish communities may result. These effects may cascade through the food web with currently unknown results (Begon *et al.*,

1996). Disruptions of native populations may also increase a system's susceptibility to invasion by exotics better suited to changing conditions (Moyle & Light, 1996). For example, Lennon *et al.* (2001) found that the high thermal tolerance of an exotic invader, *Daphnia lumholtzi*, may allow it to out-compete native *Daphnia* species through higher reproductive rates at increased temperatures. Invasion by exotic species is an important cause of extinctions, food web disruption, and loss of biological diversity (Moyle & Light, 1996).

Here, we examine temperature responses, as measured through reproductive rates, for two laboratory populations of *Daphnia pulex* acclimatized to different temperatures. *Daphnia* are ectothermic—their metabolic processes are dependent on the temperature of their surroundings. Thus many of their life history traits, including reproductive rates, are largely temperature dependent. Despite this temperature dependence, individuals that are forced to live in sub-optimal temperatures for a time will often become “acclimatized” to that temperature and perform better at that temperature than un-acclimatized individuals (Schmidt-Nielsen, 1997). Thus, we predicted that *D. pulex* hatched in warm water would show higher reproductive rates in warm water than *D. pulex* hatched in cool water. Furthermore, we predicted that those hatched in cool water would have higher reproductive rates in cool water than *D. pulex* hatched in warm water.

Hatching Temperatures	Treatment Temperatures				
	5°C	10°C	20°C	25°C	30°C
10°C	8	9	10	11	9
20°C	13	14	10	14	13

Table 1. Number of individual *D. pulex* in each cohort for all experimental treatments. Neonates were transferred to experimental treatments within 24 hours of hatching.

METHODS

Forty gravid *D. pulex*, acclimated to laboratory conditions at approximately 20°C, were obtained from Carolina Biological Supply. In order to acclimatize their offspring, 20 of these brood mothers were placed in individual 50mL tubes of 10°C water (“cool”); the remaining 20 were placed in individual 50mL tubes of 20°C water (“warm”). These temperatures were selected to be representative of broad “cool” and “warm” temperature regimes used in other studies (Bottrell, 1975). All water used throughout the course of the experiment was filtered stream water. These animals were fed ≈0.5mL of dilute *Chlamydomonas reinhardtii* daily. For the next 5 days, offspring of the brood mothers were collected and categorized according to the temperature of water in which they were born (i.e. 10° and 20°C). In total, 114 offspring were collected.

The offspring were individually transferred to 50mL tubes of water of different temperatures (5°, 10°, 20°, 25°, and 30°C). These temperatures were chosen based on equipment availability to represent a broad range of temperatures that *Daphnia* encounter in temperate climates. Approximately 10 cool offspring and 13 warm offspring were subjected to each water temperature (Table 1). Offspring were maintained in temperature- and light-controlled incubators on a 16:8 hour light-dark cycle. The offspring were fed ≈ 0.5mL of *Chlamydomonas* and *Chlorella* daily. Algal concentrations were maintained at levels sufficient for optimal growth, reproduction and survival; concentrations were the same for all treatments on any given day. The water in the offspring’s 50mL tubes was changed every two days with filtered water of the same temperature in order to prevent excess bacterial growth.

The offspring were observed for 13 days. At each daily feeding, offspring production, brood size and survivorship were recorded. From these observations, life tables were calculated. Researchers commonly use these tables to quantify reproductive rates. To calculate the net reproductive rate (R_0) for each temperature treatment, the equation:

$$R_0 = \sum l_x m_x$$

was employed where l_x is the proportion of the original treatment cohort surviving from day ($x-1$) to day (x), and m_x is the fecundity of each survivor. Using R_0 , we also determined cohort generation time (T_C) and the intrinsic rate of increase (r). All equations used in calculating life table parameters can be found in Begon et al. (1996).

Results

D. pulex from the cool and warm cohorts did not reproduce in the 5°C and 10°C treatments during the course of the experiment. Life tables were compiled for both cohorts in the 20°C, 25°C and 30°C treatments only.

The warm cohort exhibited the same number of days to first reproduction at 20°C (7.0 ± 0.0 days: mean \pm sem) as the cool cohort did at 25°C and 30°C (7.0 ± 0.0 days and 7.0 ± 0.47 days, respectively). The cool cohort had a larger number of days to first reproduction at 20°C (8.3 ± 0.3 days) and the warm cohort showed a short time to first reproduction in 25°C (5.6 ± 2.1 days). However, at 30°C, the warm cohort took the longest time of any group (8.8 ± 0.47 days) to reach first reproduction (Figure 1).

The warm cohort exhibited a very high net reproductive rate (R_0) at 20°C (38 offspring per female); R_0 decreased sharply and relatively linearly to a midpoint of 22 offspring at 25°C and a low of 3.1 offspring at 30°C. The cool cohort also decreased from 20°C to 30°C, though the decrease was smaller (14.5, 6.3 and 5.3 offspring for 20°C, 25°C, and 30°C respectively). In 20°C and 25°C, R_0 was much lower for the cool cohort, but in 30°C the 10°C cohort had a slightly higher rate than the warm cohort.

The warm cohort showed the shortest cohort generation time (T_C) at 25°C (8.61 days)

and had somewhat longer generation times of 10.0 and 9.9 days at 20°C and 30°C. The cool cohort showed similar results at 20°C and 25°C, but had a much shorter T_C (7.5 days) at 30°C (Figure 2). The warm cohort had a very high intrinsic rate of increase (r) at 20°C and 25°C (0.363 and 0.358 individuals/female/day) and a much lower r (0.114 individuals/female/day) at 30°C (Figure 3). The cool cohort displayed intermediate r -values across the treatments: slightly lower at 25°C (0.210 individuals/♀/day) and slightly higher at 20°C (0.263 individual/female/day).

The mean cumulative number of offspring increased sharply for the warm cohort at 20°C and 25°C; the rate of offspring production was slightly higher and more uniform at 25°C (Figure 4). The warm cohort had a dramatically lower cumulative number offspring at 30°C. The cool cohort showed intermediate, less differentiated values across all three treatments (Figure 4).

DISCUSSION

We hypothesized that acclimatized *D. pulex* would show maximal reproductive rates near the temperatures to which they were acclimatized. The failure of the warm cohort to reproduce in the 5°C and 10°C treatments supports this hypothesized temperature-fecundity correlation. The warm cohort exhibited a temperature optimum between 20°C and 25°C. The number of days to first reproduction showed no difference between these two temperatures (Figure 1). Net reproductive rate was higher at 20°C, as was intrinsic rate of increase (Figure 3). Cohort generation time and mean cumulative number of offspring were both better at 25°C (Figures 2,4). This optimal temperature range has been observed in several studies, including Yurista & O'Brien (2001) and Bottrell (1975).

The decreased fecundity of the warm cohort in the 30°C treatment contrasts with the hypothesized correlation of temperature and reproduction. According to Moore *et al.* (1996), reproduction and survival rates for many species of *Daphnia* tend to decrease at temperatures above 25°C. This response can be attributed to a variety of physiological effects observed at high temper-

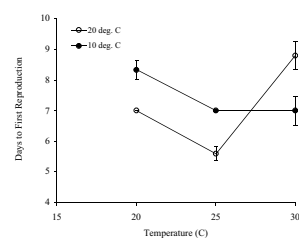


Figure 1. Number of days (from hatching) to first reproduction for the six reproducing cohorts of *Daphnia pulex* examined. The 10 deg. C line represents those cohorts hatched in 10oC water and the 20 deg. C line represents those hatched in 20oC water. Temperatures on the x-axis are temperatures of treatments used to establish life table data.

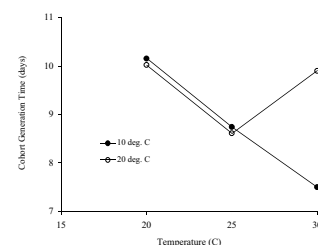


Figure 2. Cohort generation time (T_c) of the six reproducing cohorts of *D. pulex*. Error is not shown as each life table experiment was performed only once. Line and x-axis temperature designations are as shown in Figure 1.

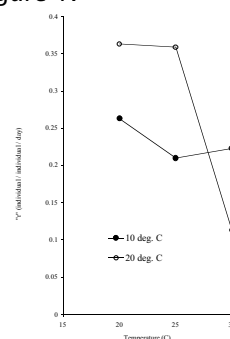


Figure 3. Intrinsic rate of increase (r) of the six reproducing cohorts examined. Error is not shown as each life table experiment was performed only once. Line and x-axis temperature designations are as shown in Figure 1.

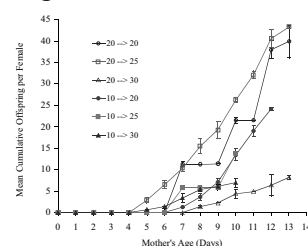


Figure 4. Mean cumulative number of offspring per female for each day of the study. Each of the six reproducing cohorts are represented individually. Data points represent means; error bars represent standard error. Means were calculated as the total offspring on a given day divided by the number of female *D. pulex* alive on that day.

atures. Though 30°C is not high enough to observe denaturation of proteins, it is high enough to cause differential changes in the reaction rates of various biochemical agents, leading to disruption of important pathways (Schmidt-Nielsen, 1997).

The failure of *D. Pulex* to reproduce in 5°C and 10°C refutes the hypothesis for the cool cohort, which was expected to show higher reproduction in colder treatments than the warm cohort. This result is not unprecedented: several studies have shown extremely low reproductive rates for *Daphnia* at temperatures less than 10°C (Lennon *et al.*, 2001; Carvalho, 1987). The moderate, poorly differentiated response of the cool cohort in the 20°C, 25°C and 30°C treatments further suggests that a simple acclimation response (to pre-hatching 10°C conditions) was not observed (Figure 4). Based on this result, we hypothesize that the cool cohort displayed a previously undiscovered response other than acclimatization. We propose that this be called a “shock response.” This may be due to the short incubation time in 10°C before placement in the treatments; this acclimatization time lasted between two and five days depending on the birth date of the experimental offspring. We suggest that this emergency response is a possible coping mechanism to deal with variability in temperature at the expense of maximal reproduction. An acclimatization response, in contrast, would be characterized by a maximal reproductive response at one temperature at the expense of adaptability to varying temperatures—such as the response observed in the warm cohort (Figure 4).

The undifferentiated response to temperature observed in the cool cohort (Figure 4) should be evaluated in light of other life table parameters (i.e. days to first reproduction, R_0 , T_c , r). The much shorter time to first reproduction and cohort generation time observed at 30°C are due to the effects of an increased number of degree days on the length of the life cycle (Figures 1,2). Some studies have shown similarly accelerated life cycles with increasing temperature (Vijverberg, 1980). These factors are balanced by decreased net reproductive rate and a

moderate intrinsic rate of increase (Figure 3), leading to the undifferentiated results for mean cumulative number of offspring (Figure 4). This trend suggests that an important part of the hypothesized shock response may be a tradeoff between generation time and brood size. Of special importance is the higher cumulative number of offspring observed for the cool cohort when compared to the warm cohort in the 30°C treatment (Figure 4). This can be attributed to the hypothesized shock response, which may confer the ability to cope with extremes of temperature. This may enable “shocked” *Daphnia* to reproduce more effectively in higher temperatures than *Daphnia* accustomed to relatively constant temperatures.

This shock hypothesis warrants further experimentation. A reasonable first step would be a similar experiment with *Daphnia* exposed to cold water for varying lengths of time. These experiments could be improved by increased duration; some studies have suggested variable reproductive rates throughout the life cycles of *Daphnia*, implicating the importance of collecting data over the full life span of the experimental individuals.

These results have important implications for performance of *Daphnia* in the event of global climate change. A mild increase in temperature in the distribution range of *Daphnia* may increase fecundity as the temperature approaches the optimum observed in this study, especially during long periods of relatively uniform temperature. The proposed short, intense storms punctuating these periods may cause rapid water temperature fluctuations in shallow systems and systems with short water residence times. These fluctuations may induce the hypothesized shock response. If so, this response could help *Daphnia* survive these rapid temperature fluctuation events. The proposed episodes of extreme high temperature would likely be detrimental to *Daphnia* accustomed to uniform temperatures, such as our warm cohort, but may be more tolerable for *Daphnia* exhibiting a shock response, especially over the short term.

These sorts of rapid temperature fluctuations are more pronounced in shallow systems and

anthropogenically altered systems. For example, systems fed by dam-controlled streams may exhibit these behaviors due to periodic cold hypolimnetic dam release. *Daphnia* from a dam-affected system could be compared to *Daphnia* from a less variable nearby system for evidence of a facultative shock response and subsequent performance in temperature extremes. Anthropogenically altered systems may be extremely useful study sites for prediction of ecosystem changes at the hands of much-touted global climate change. ■

REFERENCES

- Begon, M., Harper, J. L. & Townsend, C. R. (1996). *Ecology*. Oxford: Blackwell Science Ltd.
- Bottrell, H. H. (1975). Generation time, length of life, instar duration and frequency of moulting, and their relationship to temperature in eight species of Cladocera from the River Thames, Reading. *Oecologia*, 19, 129-140.
- Carvalho, G. R. (1987). The clonal ecology of *Daphnia magna* (Crustacea: Cladocera): II. Thermal differentiation among seasonal clones. *Journal of Animal Ecology*, 56, 469-478.
- Chen, C. Y. & Folt, C.L. (1996). Consequences of fall warming for zooplankton overwintering success. *Limnology and Oceanography*, 41, 1877-1886.
- Feddema, J. J. & Mather, J. R. (1992). Hydrological impacts of global warming over the United States, p. 50-62. In S. J. Majumdar *et al.* (eds.), *Global Climate Change Implications, Challenges, and Mitigation Measures*. Pennsylvania Academy of Science.
- Hansen, J. *et al.* (1988). Global climate changes as forecast by Goddard Institute for Space Studies three-dimensional model. *Journal of Geophysical Research*, 93, 9341-9364.
- Lennon, J. T., Smith, V. H. & Williams, K. (2001). Influence of temperature on exotic *Daphnia lumholtzi* and implications for invasion success. *Journal of Planktonic Research*, 23, 425-434.
- Moore, M. V., Folt, C. L. & Stemberger, R. S. (1996). Consequences of elevated temperatures for zooplankton assemblages in temperate lakes. *Archiv fur Hydrobiologie*, 135, 289-319.
- Moore, M. V. *et al.* (1997). Potential effects of climate change on freshwater ecosystems of the New England/Mid-Atlantic region. *Hydrological Processes*, 11, 925-947.

Moyle, P. B. & Light, T. (1996). Biological invasions of fresh water: Empirical rules and assembly theory. *Biological Conservation*, 78, 149-161.

Schmidt-Nielsen, K. (1997). *Animal physiology: adaptation and environment*. Fifth ed. Cambridge: The Cambridge University Press.

Vijverberg, J. (1980). Effect of temperature in laboratory studies on development and growth of Cladocera and Copepoda from Tjeukemeer, The Netherlands. *Freshwater Biology*, 10, 317-340.

Yurista, P. M. & O'Brien, W. J. (2001). Growth, survivorship and reproduction of *Daphnia middendorffiana* in several Arctic lakes and ponds. *Journal of Plankton Research*, 23, 733-744.

ACKNOWLEDGEMENTS

The authors would like to thank Jay Lennon for his help in lab and his aid in revising this paper. Also, Kate Schofield for introducing us to the world of aquatic ecology and Craig Layne for his tireless interest and practical help.

ABOUT THE AUTHORS

Liza Pfaff is a '99 and an environmental and evolutionary biology major & chemistry minor. During her hiatus from school she trained horses and was a rehabilitator at one of Wisconsin's largest wildlife rehabilitation facilities. After Dartmouth, she plans on going to veterinary school so she can continue her work with wildlife.

Joel Wickre is an '03 environmental biology major pursuing ecotoxicology and environmental health. He is currently organizing a bird punk band. "At first I wanted a nice choral sound and auditioned a bunch of robins and chickadees," he said, "but I soon discovered that jays can really wail."

Sierra Moldovan is an '02 and is majoring in biology. She plans on taking a couple years off before she continues her education towards a career in Forensic Science. Eventually, she hopes to return to Eagle River, Alaska, where she grew up.

Submission Guidelines

The DUJS welcomes all undergraduate submissions of science-based papers and articles. All submissions must adhere to a few guidelines:

1. The length of the article must be 3000 words or less.
2. A professor must acknowledge the validity of the article. This can be done via Blitzmail.
3. Any co-authors of the paper must approve of the submission to the DUJS.
4. References and citations must follow APA (American Psychological Association) guidelines.

Submissions should be received by Monday, October 15, 2001.

The exact, updated deadline and a more detailed version of these guidelines, complete with examples, are available at <http://www.dartmouth.edu/~dujs/submissions.shtml>.

WRITING PHILOSOPHY

The DUJS is open to all types of submissions. We examine each article to see what it potentially contributes to the Journal and our goals. Our aim is to attract a diverse audience in terms of scientific background and interest. To this end, articles generally fall into one of the following categories:

Hard Research

This type of article parallels those found in professional journals. An abstract is expected, as well as clearly defined sections of problem statement, experiment, data analysis and conclusions. The intended audience is expected to have interest and general knowledge of that particular discipline.

Review

A review article is typically geared towards a more general audience and explores an area of scientific study, e.g. methods of cloning sheep, a summary of options for the Grand Unified Theory, etc. It does not require any sort of personal experimentation by the author. A good example could be a research paper written for class.

Reflection

A reflection article resembles a popular science article or an editorial. It can examine the interplay between science and society, recall the experiences of your failed summer research, or comment on how you perceive the scientific community. These articles are aimed at a general audience and should include explanations of concepts that a basic science background may not provide.

While your article should be submitted as close to final form as possible, the Editorial Board works closely with authors to refine the work into publishable form.

DETAILS AND TECHNICALITIES

Citations MUST be in APA format. The exact formats for various types of sources can be found on our website and in the Sources Handbook.

- The article must be submitted electronically by email to dujs@dartmouth.edu with the subject header: Spring Submission. It can be in any major word processor format. Either Macintosh or PC are acceptable.
- Chemical structures must be in the format specified by the Journal of Organic Chemistry. Complete specifications can be found at <http://pubs.acs.org/instruct/illus.html>.
- Graphs must be accompanied by the original Excel (or other database) worksheet.
- Graphics must be submitted in at least 300 dpi (preferably 600 dpi). TIFF, EPS, or PICT formats are acceptable.

For more examples of these details and specifications, please see our website:

<http://www.dartmouth.edu/~dujs/>