

Effects of constant and stepwise changes in temperature on the species abundance dynamics of four cladocera species

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ABSTRACT

Key-words:
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effects,
realized niche

Laboratory experiments with natural zooplankton communities were carried out to study the effects of two contrasting temperature regimes: constant temperature (15, 20, and 25 °C) and graded changes in temperature. The graded regime consisted of repeated sustained (three weeks) controlled stepwise temperature changes of 5 or 10 °C within 15–25 °C on the population dynamics of four dominant species of lake littoral zooplankton, *Daphnia longispina* (Müller, 1785), *Diaphanosoma brachyurum* (Lievin, 1848), *Simocephalus vetulus* (Müller, 1776) and *Chydorus sphaericus* (Müller, 1785). The results show that controlled stepwise changes (positive or negative) in temperature within the ranges of 15–20, 20–25, and 15–25 °C can exert either stimulating or inhibitory effect (direct or delayed) on the development of *D. longispina* and *S. vetulus* populations. The development of *D. brachyurum* and *Ch. sphaericus*, both more stenothermophile, was only stimulated by a stable elevated temperature (25 °C). These results support the previously formulated hypothesis that, in determining the ecological temperature optimum of a species within a natural community, it is not enough to define its optimum from constant, cyclic or random temperature fluctuations, but also from unidirectional stepwise changes in temperature. These stepwise changes may also induce prolonged or delayed effects.

RÉSUMÉ

Effets de changements graduels en température sur la dynamique de quatre espèces de cladocères

Mots-clés :
température,
optimum
écologique,
Cladocère,
changements
graduels,
effets prolongés,
niche « réalisée »

Des expériences de laboratoire sur des communautés naturelles de zooplancton ont été conduites pour étudier les effets de deux régimes contrastés de température : température constante (15, 20, 25 °C) et changements graduels de température. Le régime graduel consistait en des changements de température par paliers contrôlés (de trois semaines) de 5 ou 10 °C entre 15 et 25 °C sur des populations de quatre espèces dominantes de zooplancton littoral lacustre, *Daphnia longispina* (Müller, 1785), *Diaphanosoma brachyurum* (Lievin, 1848), *Simocephalus vetulus* (Müller, 1776) and *Chydorus sphaericus* (Müller, 1785). Les résultats montrent que les changements par paliers contrôlés (positifs ou négatifs) en température dans les gammes 15–20, 20–25 et 15–25 °C peuvent exercer un effet soit stimulant, soit inhibiteur (immédiat ou retardé) sur le développement des populations de *D. longispina* and *S. vetulus*. Le développement

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de *D. brachyurum* et *Ch. sphaericus*, tous les deux sténo-thermophiles, était stimulé seulement par une température élevée stable (25 °C). Ces résultats confirment l'hypothèse formulée auparavant que, dans la détermination de l'optimum thermique d'une espèce d'une communauté naturelle, il ne suffit pas de définir son optimum à partir de températures constantes, ou de fluctuations cycliques ou aléatoires, mais aussi par des changements de température graduels. Ces changements graduels peuvent également produire des effets prolongés ou retardés.

INTRODUCTION

Temperature directly influence the rate of most biochemical processes in organisms, especially ectotherms, as well as the abiotic properties of the environment (Loiterton *et al.*, 2004), hence it has attracted a lot of attention from ecologists (Angilletta, 2009). Species temperature optima of ectotherms have been invariably defined as the body temperature for which maximum metabolism or normal daily activities occur (Prosser and Brown, 1967; Angilletta *et al.*, 2002, p. 250; IUPS Thermal Commission, 2003, p. 91).

The concept of "ecological optima" is comparable to the multivariate niche concept of Hutchinson (1957). Most of the research on ectotherm temperature optima has focused on individual or species specific response to temperature independently of other factors, equivalent to defining the "fundamental" niche of the species. However, in nature, the fundamental niche of the species may be displaced (to what is called the "realised" niche) in the presence of other species or different environmental conditions (Tilman *et al.*, 1986; Kreutzer and Lampert, 1999).

Moreover it was shown in many species, that optimum values differ for different physiological functions (Dent and Lutterschmidt, 2003; Rodnick *et al.*, 2004) and biochemical processes (Gamperl *et al.*, 2002) in the same organism. These values also depend on ontogenetic stage (Du *et al.*, 2007), sex (Melanie and Shine, 1999; Hernandez *et al.*, 2002), body size (Hoelker, 2003), season of year, time of day (Svirskiy and Valtonen, 2002), satiety (Giebelhausen and Lampert, 2001) and general physiological state (Novinger and Coon, 2000). It was also shown, that rates of growth and development differ under various conditions (Fisher and Edwards, 2002).

Hence, despite the large number of experiments involving temperature, and our increasing autecological knowledge, species response to temperature changes in natural communities are often not predictable due to the complexity of the natural systems (Schiel *et al.*, 2004).

Many studies have been devoted to research the influence of the rhythmic diurnal thermoperiods on different functions of ectothermic animals (*e.g.* Eubank *et al.*, 1973; Merkel, 1977; Sweeney and Schnack, 1977; Humpesch, 1982; Joshi, 1996; Dong *et al.*, 2006, 2008; Du *et al.* 2009). The influence of quickly oscillating temperatures was also investigated (Shelford, 1927; Sushchenja, 1978; Schmidt, 1981; Behrens *et al.*, 1983). These studies modelled natural changes in temperature, where temperature usually undergoes regular diurnal variations, frequently superimposed by irregular fluctuations.

This may explain why fluctuating (astatic) temperature regimes may be more favorable to a species than constant temperature (Odum, 1971; Dajos, 1975; Meyers, 1984; Konstantinov, 1993; Konstantinov *et al.*, 2000; reviewed in Verbitsky, 2008), although neutral or negative results have also been reported (Costlow and Bookhout, 1971; Thorp and Hoss, 1975; Sharitz and Luvall, 1978; Thorp and Wineriter, 1981; Du *et al.*, 2009). For example, small and medium temperature fluctuations accelerated the growth of sea cucumbers (*Apostichopus japonicus* Selenka) while the large temperature fluctuation retarded growth (Dong *et al.*, 2006, 2008).

While there has been a number of studies comparing the effect of constant and cyclic temperature regime on individual species metabolism, development or population dynamics (*e.g.* Khan, 1965; Barnes and Barnes, 1969; Sharitz and Luvall, 1978) very few have focused on

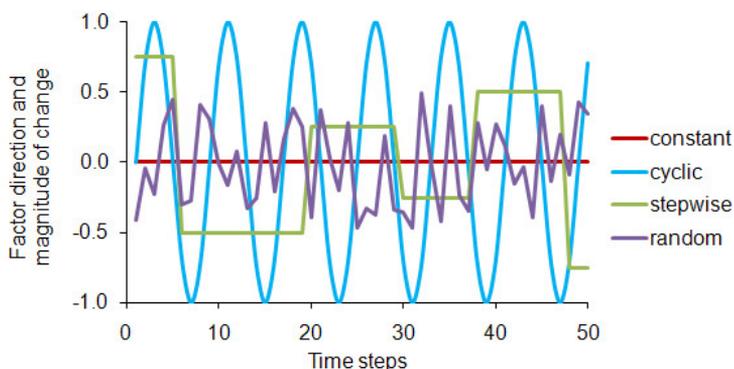


Figure 1

The variability in environmental factors may follow different regimes: cyclic, constant, stepwise, random which may be characterized by direction, magnitude, frequency, duration, timing and rate of change.

Figure 1

Les variations des facteurs environnementaux peuvent suivre différents régimes : cyclique, constant, graduel, aléatoire, qui peuvent être caractérisés par leurs direction, amplitude, fréquence, durée, rythme et taux de changement.

arrhythmic (random) temperature changes (e.g. Thorp and Wineriter, 1981), despite the fact that inhabitants of both undisturbed and thermally altered water systems may be exposed to rapid rate of change and sometimes unpredictable for individual temperature shifts.

Stepwise changes in temperature have received scant attention despite the increasing threat and occurrence of heat (or cold) waves with climate change. For example, the 2010 summer heat wave has surpassed all temperature records in Russia. Predicting the ecological response to such unpredictable change and extreme weather conditions remains a challenging task. The use of experimental microcosms may allow testing predictions of temperature changes on species, communities and ecosystem dynamics.

Hence there is a need to manipulate the temperature regimes (constant, cyclic, stepwise, random; Figure 1) as well as its characteristics (such as direction, magnitude, frequency, duration, timing and rate of change). Here the focus will be on sudden (unpredictable), sustained stepwise changes (which may resemble change in weather patterns) and study its effect on the population dynamics of species from natural communities to move towards a more predictive ecology of natural systems.

The purposes of this research were the following: (1) describe the effects of stepwise sustained (three weeks) controlled temperature shifts (relative to constant temperature controls) differing in magnitude (5 or 10 °C) and direction (positive or negative) on the dynamics of experimental populations of freshwater zooplankton species from a natural assemblage; (2) investigate influence of the recovery period after the termination of treatment effects; and (3) on the basis of the results and previous researches, state our understanding of the concept of temperature optimum for ectotherms. The concept itself may be applied to any ecological factors (e.g. water discharge in river ecosystems, Poff and Zimmerman, 2010).

MATERIAL AND METHODS

The population responses of dominant zooplankton species to graduated temperature influences were studied in long-term experiments (lasting more than 63 days) on microcosms created in 45 L aquariums (58×30×26 cm). These aquariums were kept in a room open to diffuse sunlight and additionally illuminated with fluorescent lamps for 16 h (from 7 a.m. to 11 p.m.). Zooplankton was collected in the littoral of the Rybinsk Reservoir (the Upper Volga basin) with a 64 µm mesh size net and released into aquariums so that their density was comparable to

Table I

Experimental design: timing of controlled stepped changes in water temperature. Shaded rows are the controlled experimental variants.

Tableau I

Dispositif expérimental : rythme des changements par paliers contrôlés dans la température de l'eau. Les lignes grisées sont les expérimentations à température constante.

Experimental variants	Time, days		
	1–21	22–42	43–63
	Temperature, °C		
1	15	15	15
2	15	20	15
3	15	25	15
4	20	20	20
5	20	15	20
6	20	25	20
7	25	25	25
8	25	15	25
9	25	20	25

natural assemblages. All large organisms (mainly insects and their larvae) were removed from the catch before the zooplankton was released in aquariums. Predatory species in zooplankton were limited to few individuals of *Polyphemus pediculus* L. Two-thirds of the water was renewed every 3–4th day, passing through a 64 μm mesh size net. To create thermostatic conditions, all aquariums were placed in plastic containers filled with water in which a certain temperature regime was maintained. Water temperature in each aquarium was adjusted according to the experimental scheme by moving it to a warmer or colder container. The time of heating or cooling ranged from 3 to 6 h, depending on the difference between the initial and final temperatures. Temperature deviations from specified values reached ± 0.3 – 1.1 °C in some days. The aquaria were continuously aerated and kept the oxygen concentration from 7.8 to 9.7 mg $\text{O}_2 \cdot \text{L}^{-1}$ (93.3 to 99.5% dissolved oxygen saturation).

The zooplankton was fed a suspension of *Chlorella vulgaris* algae, which was added during water replacement to a concentration of $1.2 \pm 0.3 \times 10^6$ cells $\cdot \text{mL}^{-1}$. In the intervening periods, it decreased by a factor of 2.5–3 but always remained above the “threshold food concentration” (Hanasato and Yasuno, 1985). The concentration of algae in the water was estimated by measuring the optical density in a KFK-2MP spectrophotometer (655 nm wave length with a 1.7 cm cell; made in Russia). The optical density was previously related to *Chlorella* cell counts (calibration curve). Measurements were taken at the time of water renewal.

The experiment was designed so as to study the effect of stepwise change in temperature on populations of natural zooplankton depending on its direction (determined by heating or cooling the water in the microcosms) and strength (the difference between the initial and final temperatures). It generally takes 1.5–2.5 weeks after the transfer from natural biotopes to microcosms for the acclimation of zooplankton where a structural reorganization of the community occurs. Hence, no manipulations were performed during the first 21 days. Three controls were set with constant water temperatures of 15 °C (control 1), 20 °C (control 4) and 25 °C (control 7). In experimental treatments, the water was heated by 5 or 10 °C relative to control 1, cooled by 5 or 10 °C relative to control 7, and cooled or heated by 5 °C relative to control 4. The controlled stepped change in temperature was maintained for three weeks (day 22 to 42). Thereafter, the temperature was adjusted to the initial values and maintained for another three weeks (day 43–63). Every experimental variants (controls and treatments) were replicated three times. The details of the manipulations are summarized in Table I.

Quantitative zooplankton samples (a total of 514) were taken at 3–4 day intervals. Each 1-L sample was concentrated to 10 mL, fixed with 4% formaldehyde solution, and processed according to standard methods (Kiselyov, 1969, including examination in Bogorov's chamber

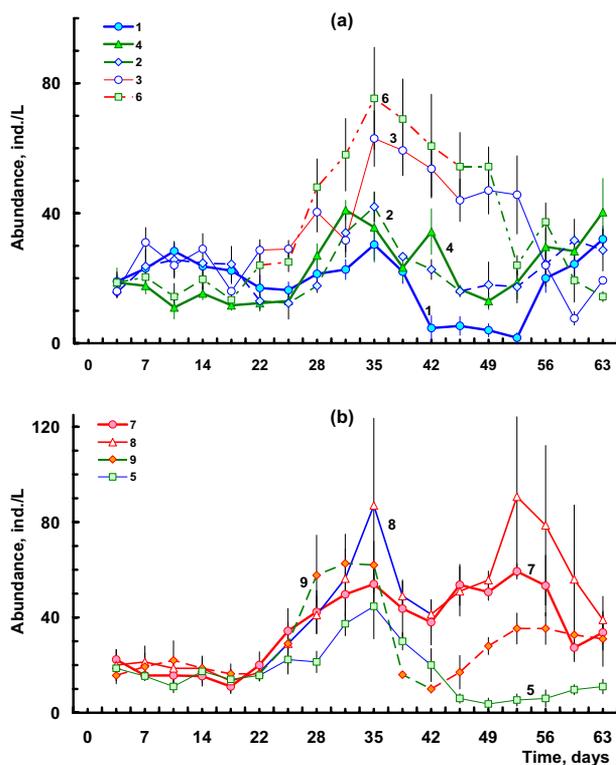


Figure 2

Dynamic of Daphnia longispina abundance in different experimental variants: (a) variants 1–5, (b) variants 6–9. 1 – Control variant with constant water temperature of 15 °C; 2 – variant, where the water was heated by 5 °C relative to control 1; 3 – variant, where the water was heated by 10 °C relative to control 1; 4 – control variant with constant water temperature of 20 °C; 5 – variant, where the water was cooled by 5 °C relative to control 4; 6 – variant, where the water was heated by 5 °C relative to control 4; 7 – control variant with constant water temperature of 25 °C, 8 – variant, where the water was cooled by 5 °C relative to control 7; 9 – variant, where the water was cooled by 10 °C relative to control 7.

Figure 2

Dynamique de l'abondance de *Daphnia longispina* dans différentes expérimentations : (a) expériences 1–5, (b) expériences 6–9. Voir le tableau I pour les régimes thermiques de chaque expérience.

under a Cytovol dissecting microscope (Carl Zeiss, Germany) to determine the species and abundance of zooplankton. Small organisms were identified under an Amplival microscope (Carl Zeiss).

Means and standard deviations (uncertainties reported throughout the manuscript) were calculated with Statistica 8 and figures were drawn in Microsoft Office Excel 6.

RESULTS

> DAPHNIA LONGISPINA

Under constant temperature, *Daphnia* populations were more abundant at high temperatures (Figures 2a and 2b). The dynamic of *Daphnia* during the first 42 days was identical during the periods of increase and decrease in abundance at all three constant temperature regimes (variants 1, 4 and 7). But greater abundance was achieved at higher temperature. *Daphnia*'s dynamic was still the same from day 43 to 63 at constant 15 and 20 °C, but not at 25 °C where the period of high abundance was on average 20 days longer, than at 15 and 20 °C. At the end of the experiment (day 63), the average abundance of *Daphnia* in all variants, irrespective of temperature, practically returned to the initial level, with differences from it or between variants lacking statistical significance.

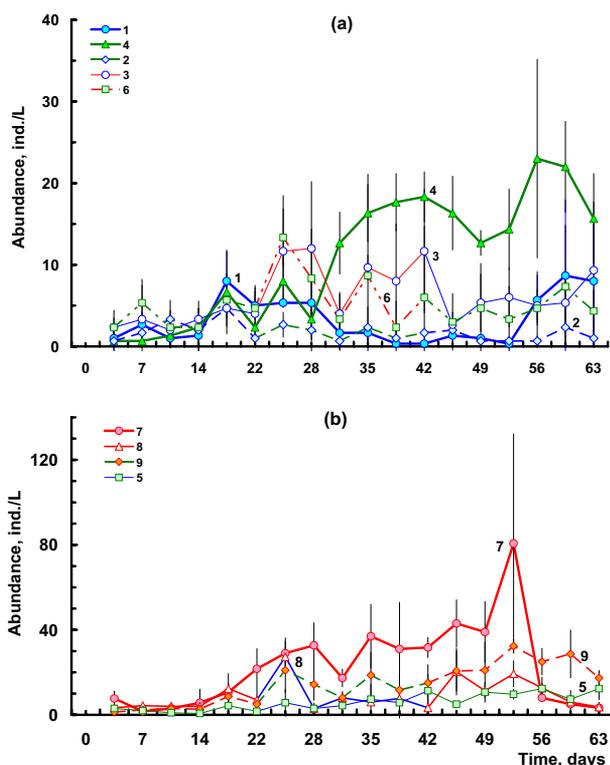


Figure 3

Dynamic of *Diaphanosoma brachyurum* abundance in different experimental variants (1–9). All symbols as in Figure 2.

Figure 3

Dynamique de *Diaphanosoma brachyurum* dans les différentes expériences (1–9). Mêmes symboles qu'en figure 2.

The pattern of abundance dynamics after water heating from 15 to 20 °C became similar to that in the control with a constant temperature of 20 °C (Figure 2a). Conversely, temperature drop from 20 to 15 °C resulted in a decrease in abundance to the level observed in control with a constant temperature of 15 °C. Water heating from 20 to 25 °C had a significant stimulating effect on *Daphnia* (Figure 2b). After reversing the temperature regime (from 25 to 20 °C), their abundance remained high for ten more days and only then decreased to the level recorded in control with a constant temperature of 20 °C; *i.e.*, a delayed stimulating effect was observed. Water cooling from 25 to 20 °C stimulated population growth in the first 14 days (Figure 2b). Both heating and cooling of water by 10 °C proved to have a strong stimulating effect on *Daphnia* populations (their average abundance was twice higher than in control with a constant elevated temperature), but the effect of heating lasted longer (11 days) (Figures 2a and 2b).

Thus the reactions of eurythermic *Daphnia* are labile and depend both on the force and direction of temperature influences. Stepwise temperature shifts in the ranges of 15–20, 20–25, and 15–25 °C, can exert both direct or extended stimulating effect and direct inhibitory effect on natural *D. longispina* populations.

> DIAPHANOSOMA BRACHIURUM

At 15 °C, *Diaphanosoma* abundance fluctuated at a low level during the whole observation period. At 20 °C, the abundance gradually increased during the first 35–40 days and subsequently stabilized at a level 15–23 ind·L⁻¹ (Figure 3a). Under constant temperature, 25 °C

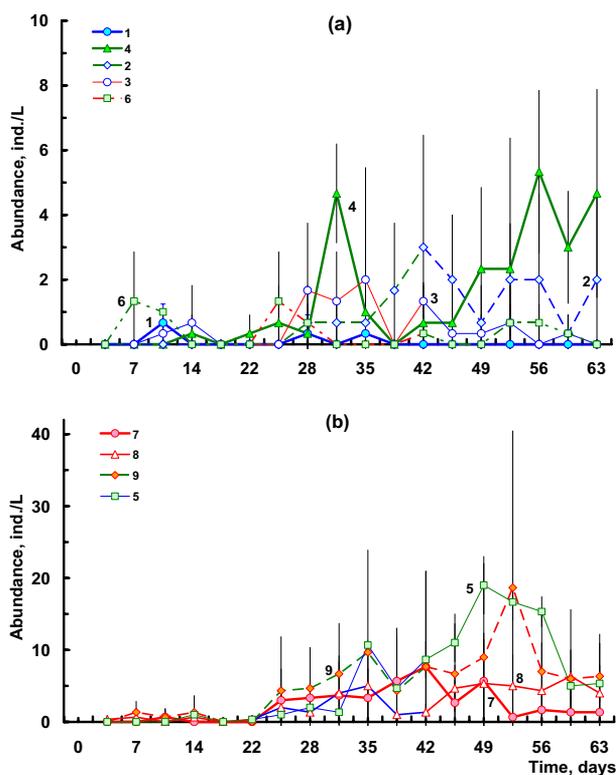


Figure 4
Dynamic of *Simocephalus vetulus* abundance in different experimental variants (1–9). All symbols as in Figure 2.

Figure 4
Dynamique de *Simocephalus vetulus* dans les différentes expériences (1–9). Mêmes symboles qu'en figure 2.

proved to be optimal for *Diaphanosoma* (Figure 3b). In this variant the abundance increased till day 53, having achieved 81 ind·L⁻¹ then sharply declined by 10 times.

Water heating from 15 to 20 °C resulted in suppressed population development (Figure 3a). Apparently, both direct and delayed inhibitory effects took place in this case. Water cooling from 20 to 15 °C also caused a significant decrease in abundance (compared to that at a constant temperature regime) (Figure 3a). Water heating from 20 to 25 °C and cooling from 25 to 20 °C retarded the growth of experimental populations (Figure 3b). In both of these treatments, a reverse temperature shift also had no effect on the pattern of abundance dynamics. Water heating by 10 °C had a slight stimulating effect on population development in the period between days 25 and 53 (Figure 3a). Water cooling by 10 °C retarded the growth of experimental populations by a factor of two to eight (Figure 3b).

Therefore, *Diaphanosoma* reached a peak of development only at a constant elevated temperature, with their abundance in all treatments being significantly lower. Alternating regimes inhibited population development, compared to that at constant regimes, and this effect manifested itself both during and after exposure.

> SIMOCEPHALUS VETULUS

Under stable temperature, at 15 °C, the abundance of cladocerans remained at the initial minimal level throughout the experiment (Figure 4a). At 20 and 25 °C, non periodic fluctuations were observed in the range 1 to 5–8 individuals·L⁻¹.

When the temperature was increased from 15 to 20 °C, the dynamics of *Simocephalus* abundance became similar to the abundance of the control with constant 20 °C temperature

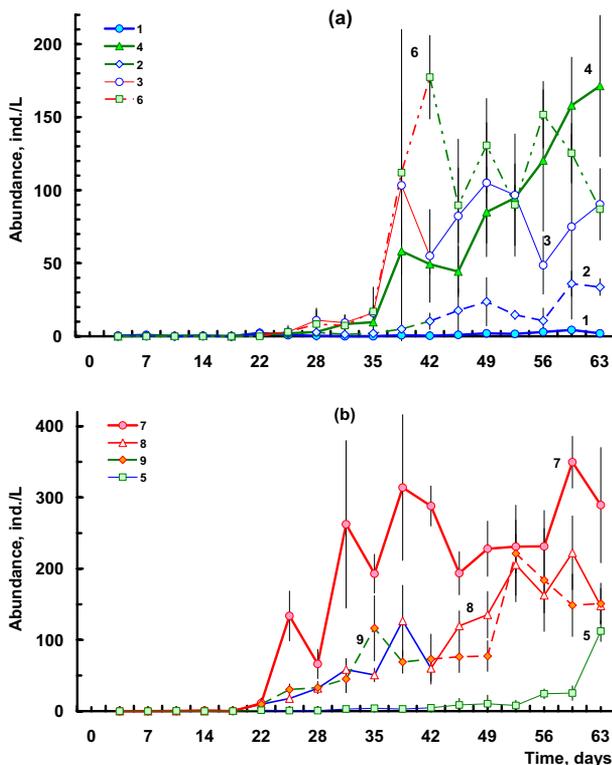


Figure 5
Dynamic of *Chydorus sphaericus* abundance in different experimental variants (1–9). All symbols as in Figure 2.

Figure 5
Dynamique de *Chydorus sphaericus* dans les différentes expériences (1–9). Mêmes symboles qu'en figure 2.

(Figure 4a). A decrease in water temperature from 20 to 15 °C also induced an increase in abundance, which continued to grow after the temperature increased back on day 42, hence a prolonged stimulatory influence was observed (Figure 4b). The heating of water from 20 to 25 °C inhibited the increase in the population abundance for a prolonged period (Figure 4a). The chilling of water by 5 °C caused a rapid increase in the population abundance (Figure 4b). The heating of water by 10 °C caused a slight increase in the population abundance (Figure 4a). After the temperature regime was changed back, the abundance reduced again to the initial minimal level. The mean abundance of the crustaceans after the chilling of water by 10 °C did not significantly differ from the abundance in the 25 °C control because of large uncertainties (Figure 4b).

Thus the maximum development of *Simocephalus* populations was observed when the water temperature decreased from 25 to 20 °C and from 20 to 15 °C. In those treatments, a prolonged stimulatory effect of temperature change was observed on the abundance of *Simocephalus*.

> CHYDORUS SPHAERICUS

Abundance of *Chydorus* under stable temperature regimes displayed higher abundance at higher temperature. This species reached the maximal development at 25 °C (Figures 5a and 5b). Thus at 20 °C the abundance increased continuously up to the end of experiment achieving 171 ind·L⁻¹. At 25 °C the abundance increased up to day 32, then fluctuated up to the end of the experiment at 194–350 ind·L⁻¹.

Abundance of *Chydorus* generally tracked the controlled and sustained changes in temperature (Figures 5a and 5b).

DISCUSSION

Daphnia longispina is a dominant species in the littoral zone of the Rybinsk reservoir. This species becomes highly abundant at temperatures above 14 °C but disappears from the plankton after water warming up to 25.8 °C (Verbitsky *et al.*, 2002). The results of this study agree with published data on *D. longispina* development in natural biotopes. It is known that *D. longispina* actively develops both in summer and in winter, it is noteworthy that it has proved to dominate in years with low summer temperatures in the Rybinsk Reservoir (Rivjer, 1986, 1992) and in winter and spring months in the Azibo Reservoir, Portugal (Geraldés and Boavida, 2004). At temperatures above 26 °C (e.g., in zones of heated water discharge from thermal power plants), the species disappears from the plankton (Elagina, 1974). Many authors have also shown that the actual growth rates of *Daphnia* species are higher at alternating temperatures than at comparable average constant temperatures (Orcutt and Porter, 1983; Manca *et al.*, 1986). The range of most favorable temperatures for *D. longispina* is 15–21 °C, and the specific growth rate of these crustaceans at constant population density does not depend on temperature within this range (Sarviro, 1985). According to Hanasato and Yasuno (1985), even-sized newborn *Daphnia* raised at 15, 20 and 25 °C show no differences in body length after 25 days, and their growth curves at these temperatures are also similar. These authors have also found *Daphnia* in the hypolimnion of Lake Lunoko (Japan) at a water temperature of 12 °C. On this basis, they conclude that *D. longispina* is adapted to life at relatively low temperatures. Some reports (McKee *et al.*, 2003) that population abundances of large bodied cladocerans, *D. longispina* and *S. vetulus* from microcosm ecosystems created to mimic shallow pond environments, were practically not affected by the 3 °C increase in temperature above ambient natural temperature.

All these results agree well with the data described above. In almost all experimental regimes with the water temperature changing within the range of 15–25 °C, the first stepwise shift by 5 or 10 °C, either upward or downward, stimulated the development of *D. longispina* populations. The only exception was the variant with water cooling from 20 to 15 °C, which proved to have no effect on the pattern of abundance dynamics.

A similar effect was described for strains of infusorians *Blepharisma* collected in various latitudinal zones and subsequently kept at 20 °C for a long period of time (Hinz and Isquith, 1974). The growth rate of these infusorians increased after temperature was raised shortly up to 30 and 40 °C and then returned to 20 °C. Also, the ambient temperature during embryogenesis in rotifers *Brachionus calyciflorus* Pallas (Galkovskaja *et al.*, 1988) and Cladocera *Daphnia magna* Straus exerts a so-called “trace” effect on growth parameters during the post-embryonic period. It should be noted, however, that under constant temperature conditions within the range of 15–25 °C, the abundance of *D. longispina* has proved to increase at higher temperatures. Thus fluctuations in abundance occurred in variants with constant regimes also there were the fluctuations of an abundance during similar periods to other variants. It is interesting, that the maximal values and cyclicity of abundance at constant temperatures were equal to those recorded in water reservoirs (e.g. Ranta and Tjossem, 1987; Manca and Comoli, 1999). The similar limits in abundance between experiments and water reservoir may suggest internal population mechanisms of abundance regulation, although a more complex regulation (interaction of top-down and bottom-up controls) in the natural environment cannot be ruled out.

> DIAPHANOSOMA BRACHYURUM

The fact that experimental populations of this species could reach the maximum level of development only at elevated temperatures is in agreement with numerous published data on its development in water bodies, which characterize *D. brachyurum* as a stenothermic thermophile (Herzig, 1984; Bertilsson *et al.*, 1995; etc.). Eie (1974) recorded this species only in

lakes located in climatic zones with relatively long and warm summers. The development of these cladocerans in the mesoeutrophic Azibo Reservoir was also observed only in the summer period (Geraldés and Boavida, 2004). Gulyas (1980) estimated the temperature optimum for this species at 19–22 °C, since he could find the first mature females only when the average water temperature exceeded 19.3 °C. In autumn, when it dropped to 15 °C, the abundance of parthenogenetic females decreased rapidly, and they disappeared from the plankton at 10–11 °C. Hanazato and Yasuno (1985) found that the growth rate of *D. brachyurum* remained unchanged within a temperature range of 20–30 °C but decreased significantly at lower temperatures between 15 and 20 °C. In the zone of heated water discharge from the Kostroma thermal power plant, an abundant development of *D. brachyurum* began only after the water temperature had reached 30 °C, sometimes even rising to 34.8 °C (Elagina, 1974). The results of experimental studies on several prevalent zooplankton species show that *D. brachyurum* is the least competitive among them (Semenchenko *et al.*, 2005). It can reach a high abundance only at a very high equilibrium concentration of food and has a low rate of population growth. After comparing our experimental data with field observations and the results of comparative studies on the competitiveness of *D. brachyurum*, it becomes evident why this species in water bodies is usually no more than subdominant even under the most favorable nutrient and thermal conditions.

> SIMOCEPHALUS VETULUS

It is a typical littoral, shallow, phytophilous species, inhabiting overgrown vegetated littoral lakes and reservoirs, and also temporary reservoirs in which significant differences of temperatures, even daily, occur (Bertilsson *et al.*, 1995; Hann and Zrum, 1997; Stansfield *et al.*, 1997). From our data, along the littoral of the Rybinsk reservoir, in spring, *S. vetulus* develops at temperatures above 14–16 °C, and the peak of abundance is during the summer months with temperatures reaching 20–25 °C.

According to our data, *Bosmina longirostris* (Müller, 1785) is the first Cladocera to increase in abundance in spring, in the littoral of the Rybinsk reservoir, when water warms up to 6–8 °C (personal observation). Upon further warming to 10–12 °C, the number of other species increases: *Daphnia longispina* (Müller, 1785), *Ceriodaphnia quadrangula* (Müller, 1785), *Diaphanosoma brachyurum* (Lievin), predatory *Polyphemus pediculus* (L.), *Chydorus sphaericus* (Müller, 1785), *Acroperus harpae* (Baird), *Alona* sp., and other species. The development of *Simocephalus vetulus* starts at temperatures of > 14–16 °C, peaking in summer at temperatures of 20–25 °C. According to van Doorslaer *et al.* (2007), the optimal temperature for *S. vetulus* is 22 °C; the stressful temperature is 26 °C. Unlike most species listed above, *S. vetulus* does not exhibit short unimodal or bimodal peaks in number. This species is a constant subdominant species.

The analysis of the abundance dynamic of *Diaphanosoma birgei* (Korinek); *Ceriodaphnia dubia* Richard, 1994; *Pleuroxus denticulatus* Birge, 1970; *Chydorus* sp.; and *Simocephalus vetulus* in (Hann and Zrum, 1997) also demonstrates the presence in all species, except for the latter, of several (one to three) short peaks of development in three summer months; in *S. vetulus*, the high number period continues from the beginning of June to mid July. Other researchers report on similar dynamic patterns (Perrow *et al.*, 1999; Balayla and Moss, 2003). There are no published data indicating that, upon changes in water temperature, the water cooling periods particularly stimulate number growth in *S. vetulus*, as was found in this study. Presumably, in natural conditions, due to the high variability of the temperature simultaneously with other factors, it is difficult to find cause and effect relationships for such interactions.

Natural populations of *S. vetulus* should develop well at water temperatures > 15 °C both at relatively stable and fluctuating temperature regimes and at sharp and strong changes in temperature. The astatic regime should be more favorable for their development than the stable regime, especially after a 4–4.5 °C decrease in temperature.

In addition to high thermal lability, *S. vetulus* possesses a relatively high oxygen lability (LaBerge and Hann, 1990) and feeding plasticity, which is confirmed by the high growth rates

of populations even at very low equilibrium concentrations of food, which results in a decrease in number being observed in other species (Semenchenko *et al.*, 2005, 2007). Moreover, upon changes in the water temperature within the diapason of 12–25 °C *S. vetulus* is able to recover its carbon assimilation rate quickly (Bevan *et al.*, 1980), which, as the authors of this paper believe, indicates the ability of this species to quickly acclimate at various temperatures.

The thermo-lability of *S. vetulus* coupled with high general ecological plasticity explain the successful coexistence of this species with other littoral species of zooplankton throughout the growing season in most water bodies with temperate climate.

> *CHYDORUS SPHAERICUS*

C. sphaericus is known as a particularly tolerant species, being able to thrive in a wide range of conditions, and to have a fairly ubiquitous distribution (Duigan, 1992; Fryer, 1993). In water reservoirs, the eurybiontic species *Ch. sphaericus* occurs over a very wide temperature range: from 2–4 °C in the ice period, where feeding but not reproduction occurs (Rivjer, 1986, 1992), to 36 °C in cooling ponds from thermal discharges (Gorobey, 1974). Moreover, massive development of this species has been recorded in the heated zone of the cooling pond of power stations observed in the period of maximum summer temperatures (Velichko, 1982). An earlier study from the same water body noted the almost complete absence of this species in cold years and the massive development in the warm years (Luferova and Monakov, 1966).

The success of *C. sphaericus* has been attributed to factors such as its physiological tolerance, its evasion of predation because of its spherical carapace and an ability to assume a planktonic lifestyle, possibly using mats or filaments of algae as its substratum (Fryer, 1968, 1993). These factors may also explain a reported dominance of *C. sphaericus* in nutrient enriched water bodies (Whiteside and Harmsworth, 1967; Hofmann, 1996; Mezquita and Miracle, 1997).

The responses of three chydorid species, *C. sphaericus* (Müller), *Alona affinis* (Leydig) and *Alonopsis elongata* (Sars) to temperature, pH and food type were previously examined (Eyto and Irvine, 2001). *C. sphaericus* had the fastest egg development time at all temperatures (8, 12, 16 or 20 °C), at all pH levels (5.0, 6.6, 8.4) and on all versions of food (algae *Chlamydomonas reinhardi*, detritus and filtered pond water containing only microorganisms < 30 µm). This is consistent to other studies that found similar egg development times of *C. sphaericus* (Bottrell, 1974; Meyers, 1984).

The universal presence of this species is also provided by its population ability to grow at a faster rate than the other species when fed on an algal culture and on filtered pond water, suggesting that in addition to using algal mats as a substratum on which to live (Fryer, 1968; Havens, 1991), it is also able to feed on bacteria and tiny detritus particles (< 30 µm) (Fryer, 1968). *C. sphaericus* is also particularly successful in nutrient enriched lakes with high phytoplankton biomass (Whiteside, 1970).

Hence, we experimentally has shown, that the abundance of Cladocera species may be stimulated not only by warming or rhythmic oscillatory regimes (as previously reported), but also by unidirectional stepwise changes in temperature (sudden heating or cooling of water).

Thus, the investigated four species can be divided into two groups based on the characteristics of their response to temperature: (1) *D. longispina* and *S. vetulus* populations which achieve maximal abundance in variable temperature regimes; and (2) *D. brachyurum* and *C. sphaericus* populations which grow faster under higher, stable temperature. Moreover, the recovery period has allowed revealing post treatment effects (prolonged temperature effects) on species abundance, reflecting population changes due to individual life expectancy and reproductive rate.

> *REVISITING THE CONCEPT OF SPECIES OPTIMA*

The above results support the previously formulated hypothesis (Verbitsky and Verbitskaya, 2007; Verbitsky, 2008) that, in determining the ecological temperature optimum of a species

Table II*Factor regimes and their characteristics.*

Tableau II

Les différents régimes et leurs caractéristiques.

	Constant ("static")	Dynamic ("astatic")		
		Cyclic	Stepwise	Random
Timing of change	n/a	regular	irregular	random
Direction	n/a	alternative	variable	random
Rate of change	n/a	variable	fastest	variable
Magnitude	fixed	variable	variable	variable
Frequency	n/a	regular	n/a	n/a
Duration	infinite	none	variable	none
Predictability	high	high	intermediate	none

n/a, not applicable.

within a natural community, it is not enough to define its optimum from constant, cyclic or random temperature changes, but also from unidirectional stepwise changes of temperature. We propose to draw a distinction between the concepts of "static" optimum (or static characteristics of an optimum) and "dynamic" optimum (or dynamic characteristics of an optimum) when defining an ecological optimum. The static optimum includes a range of optimum factors' values on tolerance scale and the "dose" of each factor corresponding to requirements of an organism and providing most favorable conditions for its life.

The dynamic optimum includes a set dynamic characteristics which provides optimum conditions for the life of an organism in natural habitats (or such conditions are necessary to be created in artificial habitats). At the time being, known dynamic characteristics include optimum parameters of periodic/cyclic changes of a factor (frequency and amplitude), their position within a range of optimum values (bottom, middle or top part), presence or absence of stimulating or inhibiting influence of stepwise changes of the factor, duration of influence of either "dose" of the factor, interval between values of "dose" and a directionality of a change of factor. Moreover, the presence and character of after-action (prolonged) effects, manifested some time after an action of optimal factor's values starts or even after it is terminated (delayed), should be taken into account (Figure 6).

Of course, the population dynamics of natural communities is also driven by other factors such as biotic interactions (*e.g.* Tilman *et al.*, 1986), food availability (Starkweather and Bogdan, 1980; McCauley and Kalff, 1981; Stemberger, 1981; Pushchina and Verbitsky, 1983; Chow-Fraser and Knoechel, 1985; Chow-Fraser, 1986; Sarviro and Verbitsky, 1988; Zurek and Bucka, 1994) and fish predation (Brooks and Dodson, 1965; Verbitsky *et al.*, 1980; Verbitsky and Verbitskaya, 1989; Cristoffersen *et al.*, 1993; Ronneberger *et al.*, 1993), as well as abiotic components such as turbidity (Zettler and Carter, 1986; Hart, 1988, 1990; Kirk and Gilbert, 1990; Kirk, 1991), nutrient status (Bays and Crisman, 1983; Hanson and Peters, 1983; Pace, 1986; Verbitsky and Verbitskaya, 2007).

But our researches of influence of others abiotic environmental factors (Verbitsky and Verbitskaya, 2007) and the analysis of the literature allows to assume, that the approach to define a real ecological optimum for ectotherms as described in this article may be applied to other environmental factors.

Table II summarizes the characteristics of the constant ("static") and dynamic ("astatic") factor regimes. The present study suggests that it is necessary to know the individual or species response to these different regimes in order to determine the biological optimum. The novel experimental design allowed demonstrating prolonged or delayed biological responses from the stepwise regime.

We assume that further investigations will reveal more characteristics and effects which directly determine a real ecological optimum in ectothermic animals, from which a more detailed concept of ecological optimum may arise. It also make it possible to estimate quantitatively

Ecological optimum of an organism/population for the certain factor

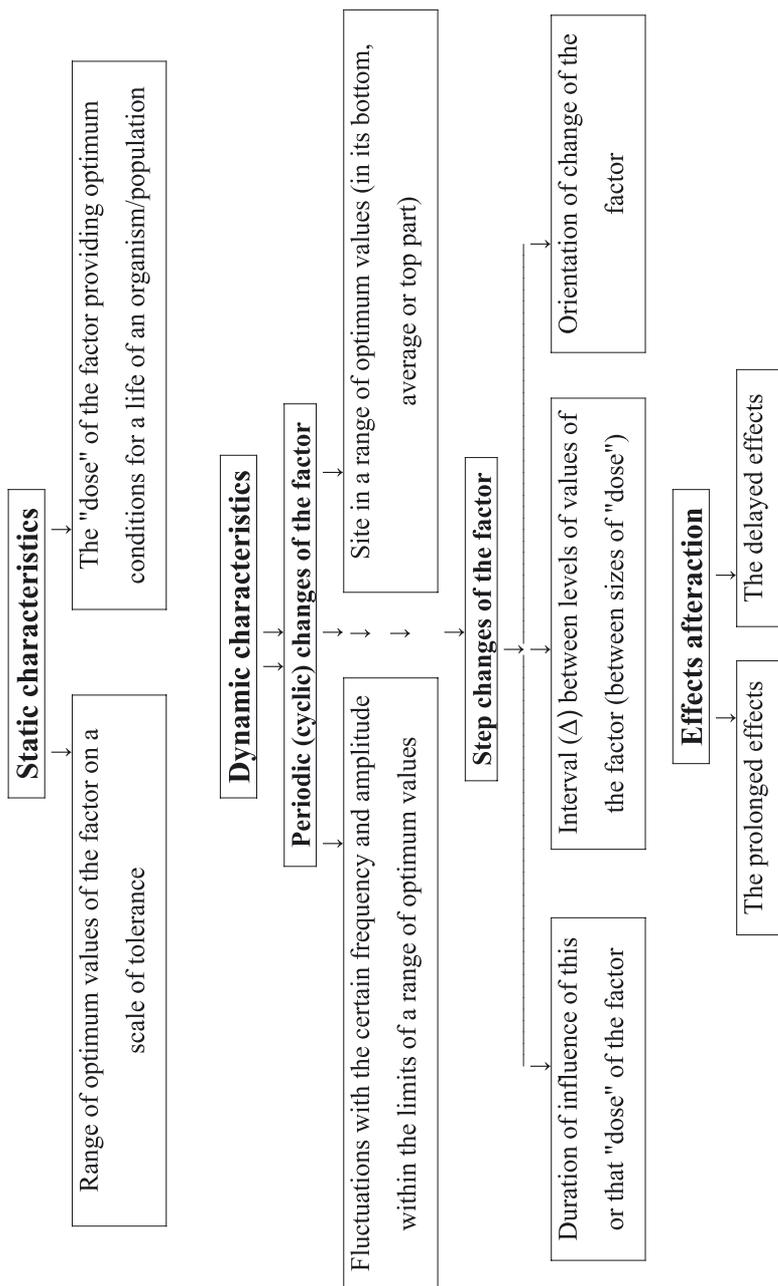


Figure 6
Scheme of the ecological optimum of an organism/population for the certain factor.

Figure 6
Schéma de l'optimum écologique d'un organisme/d'une population pour un facteur donné.

the contribution of various characteristics of environmental factors to formation of ecological optima for organisms and populations.

> **IMPLICATIONS FOR MANAGEMENT**

The approach outlined here, could be especially productive for an introduction of new species into aquaculture, as well as for optimization of cultivation regimes for aquatic and terrestrial ectothermic organisms.

Besides, this study provides critical evidence of Cladocera species response to the predicted increasing risks in sharp changes and extreme weather conditions due to climate change, as observed in summer 2010 in Russia, where the water temperature of the River Volga (Yaroslavl area, Gorki reservoirs) heated up to 29–30 °C in July. Our experiments allow to make predictions regarding the single effect of temperature on Cladocera and probable consequences of such unexpected strong temperature impacts for water communities.

CONCLUSIONS

It is known that the response of species on temperature is largely determined by their environment. On the basis of the research carried out, it is shown for the first time, that increase in Cladocera abundance can be stimulated not only by warming up or rhythmic oscillatory modes, but also sustained unidirectional stepwise changes of temperature. Thus, the results of our study clearly illustrate distinctions in temperature ecological strategy of the studied species of Cladocera plankton, living in the same water reservoir.

These results support the previously formulated hypothesis that, in determining the ecological temperature optimum of a species within a natural community, it is not enough to define its optimum from constant or unidirectional temperature changes, but also from fluctuating step changes of temperature. Besides it is necessary to consider possible prolonged or delayed biological response to sudden stepwise changes in environmental conditions as expected under climate change.

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