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## Cyclicality of Long-term Population Dynamics in Damselflies of the Genus *Coenagrion* (Odonata, Zygoptera) in the Lake Chany Basin

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**Abstract**—The cyclicality of population dynamics of abundance has been analyzed in sympatric adult populations of three odonate species monitored for long time (1980–2010) in the Lake Chany basin (Western Siberia). The spectra of odonate population dynamics have been constructed for the first time and shown to be species-specific: each species has its own population cycles, and if the cycles are similar, interspecific differences manifest themselves in the relative power of these cycles. These differences provide for separation of species in time, reducing the stress of competition between them. The population rhythms of all studied species show synchronicity with natural rhythms that are important to them, such as fluctuations of climatic parameters (2–3 year cycles) and hydrological parameters of Lake Chany (2–4-year cycles).

**Keywords:** Odonata, long-term population dynamics of abundance, population cycles, population rhythm spectrum, southern Western Siberia, Lake Chany basin, forest–steppe

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Data on the results of censuses of a particular species shown on a time scale with a constant step are commonly used in chronoecology to represent population dynamics. Long-term population dynamics of abundance are to this day often described by this simple method. When it is subsequently compared to other dynamic processes, correlation coefficients are usually calculated in the hope that high values of these coefficients will make it possible to state that the processes are linked. But this is not necessarily true from the mathematical point of view. Using classical chronograms and correlation coefficients only indirectly reveals any patterns of population size changes and, on the whole, say little about functional relationships.

Long-term series of data on population dynamics can be analyzed by another, more adequate method: using spectral analysis, based on the notion of cycles (rhythms, harmonic or periodical components) in the dynamics of any population. Spectral analysis has been used for processing time series for about half a century (Jenkins and Watts, 1971; Erdakov, 1991; Sollberger, 1968; Binkley, 1973). In the late 20th century it was vigorously debated whether populations can be either cyclic or noncyclic (Erdakov et al., 1990), but

now there are no more doubts about the existence of cycles in the dynamics of any population (Beletskii, 1992, 2011; Chernyavskii and Lazutkin, 2004; Simonovich et al., 2008). Any population demonstrates a very complex polyperiodical dynamics. In practice, it is very rarely possible to find population dynamics that can be described by a regular or almost regular sinusoid. The intricate curve of population dynamics usually includes many hidden periodical components. Population cycles are endogenous in origin, being determined by intrapopulation processes rather than external processes, such as geophysical rhythms; at the same time, for a population rhythm not to be decaying, it should be constantly connected to a stable external (e.g., climatic) cycle (Erdakov, 1991).

The presence of its own rhythms is necessary for any population as a mechanism of adaptation to cyclic changes in the environment that are important to this population. Almost all environmental influences are cyclic. A population can adapt to any external rhythms by synchronization (extension of its own rhythm). Population dynamics differentiates environmental influences and adjusts itself to particular external rhythms it needs. These rhythms are fairly easy to recognize, because the population should have internal harmonics with a similar period.

<sup>†</sup> Deceased.

Cycles of population dynamics of abundance have been described and their parameters determined for many animal populations (Maksimov, 1984; Beletskii, 2011; Erdakov, 2011; Koltunov and Erdakov, 2013). Here, odonate populations are considered in this aspect for the first time. The purpose of this study is to describe and analyze the chronoecological structure of long-term dynamics in adult populations of three damselfly species of the genus *Coenagrion*: to make chronograms and species spectra of long-term abundance dynamics, calculate periods and their power in the population dynamics of each species, analyze chronograms and spectra with regard to distinctive ecological features of species, and reveal the synchronization of each species to natural rhythms of the habitat.

The above species were chosen for the following reasons: (1) they are closely related and therefore similar in specific ecological features and size parameters; (2) they are sympatric species in the study area; and (3) their abundance remained medium to high over the entire study period, which reduced the probability of calculation errors associated with differences in abundance between years (very low estimations, many zero estimations). However “close” these species are, they coexist in a rather friendly manner in almost the same space and time.

## MATERIAL AND METHODS

The chronoecological analysis was based on the census data by A.Yu. Kharitonov and O.N. Popova on the abundance of odonates in southern Western Siberia (the central part of the Baraba forest–steppe) in 1980 to 2010. The quantitative censuses were taken in the same period of the year and in the same 272-km<sup>2</sup> area adjacent to the northeastern bank of Lake Malye Chany, the so-called Chany test area (54°32′–54°39′ N, 78°06′–78°19′ E).

The imagoes of three abundant species of damselflies (Zygoptera) of the genus *Coenagrion* Kirby, 1890 have been studied: *C. armatum* (Charpentier, 1840), *C. lunulatum* (Charpentier, 1840), and *C. pulchellum* (Vander Linden, 1823). Four other species of this genus also live in the Chany test area, but they are either rare (two species) or occur sporadically (two species).

The data for calculating abundance (ind./m<sup>2</sup>) have been obtained mainly by two methods: mass marking and recapture of adult odonates (Haritonov, 1990; Corbet, 1952; Parr, 1972) and visual censuses on band transects (Popova and Haritonov, 2010). We mostly use in this study the term “abundance” instead of “density,” because changes in density adequately reflect changes in the number of individuals (Ravkin and Luk’yanov, 1976).

The water level in Lake Chany has been monitored by the local weather station since 1899. We calculated cyclicity from data on the water balance and level of the lake over the study period (31 years). In addition, we used published data on the dynamics of the water level in Lake Chany calculated also by spectral analysis, but for a longer period (Savkin et al., 2005).

The time series were presented as chronograms and, in addition, analyzed for presence of hidden harmonic components. Chronograms and spectra of rhythms in the dynamics of abundance were constructed for each species, and the periods and powers of the harmonic components were calculated for each species spectrum. The calculations were performed by standard methods (Erdakov, 2011; Koltunov and Erdakov, 2013) using computer programs owned by the Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences. The data were processed by the Welch method, windows 8, 16, and 24 with 95% overlap. The most stable patterns of spectral density (power) distribution were selected. The statistical processing was performed using the program Past.

## RESULTS AND DISCUSSION

*Coenagrion armatum* and *C. lunulatum* are smaller than *C. pulchellum*: they do not reach even the minimum size of the latter species (Table 1). The average body weight in all three species is similar, because *C. pulchellum* is slenderer and more gracile than the other two species. Body length is the more stable of the two studied characters: the coefficient of its variation is 4.3% in *C. armatum*, 3% in *C. lunulatum*, and 2.8% in *C. pulchellum*.

The larvae of these damselflies are fairly tolerant to different environments and colonize both various closed water bodies (lakes and wetlands) and bays of watercourses; they are not sensitive to pollution and

**Table 1.** Size parameters of three species of the genus *Coenagrion*

Species	<i>n</i>	Body length, mm				Hindwing length, mm			
		min–max	<i>M</i>	<i>m</i>	<i>CV</i> , %	min–max	<i>M</i>	<i>m</i>	<i>CV</i> , %
<i>C. armatum</i>	40	28.0–33.5	30.5	0.2	4.3	15.0–20.0	17.5	0.2	7.2
<i>C. lunulatum</i>	40	29.0–33.0	31.0	0.2	3.0	16.5–21.0	18.4	0.2	5.8
<i>C. pulchellum</i>	45	33.0–37.5	34.6	0.2	2.8	17.0–21.5	19.0	0.2	6.4

water mineralization but have a need for macrophyte beds (Belyshev, 1973). However, they have some species-specific features: *C. armatum* is indifferent to water body type as long as the principal condition is met: aquatic vegetation should be abundant; *C. lunulatum* prefers closed water bodies and occurs in watercourses only in bays; in contrast, *C. pulchellum* most readily colonizes flowing water bodies (but not streams with an appreciable current). Adults of the three species differ in their preferences for terrestrial vegetation: *C. armatum* and *C. lunulatum* prefer relatively low herbaceous plants, whereas *C. pulchellum* prefers trees and shrubs. Accordingly, the first two species mainly occur in open areas, represented in the Baraba forest–steppe by meadow–steppe low ridges and floodplain meadows, and the third species prefers small birch–aspen forests and their edges. Therefore, in *C. armatum* high variability in linear parameters of the body is combined with a broad spectrum of habitat preferences, whereas in *C. lunulatum* and *C. pulchellum* relative stability of linear body size is combined with more strict habitat requirements. Interestingly, the *C. armatum* population inhabiting one of the lakes in the Chany test area has been found to be differentiated into two intrapopulation topic groups (one concentrating in stretch of lake and the other in reed edge), which increasing the holding capacity of the environment for this species as a whole (Popova and Haritonov, 2014). In short, although the combination of environmental conditions preferred by the three species is rather similar, each of them has its own specific features at both larval and adult stages, which should alleviate competition for environmental resources between sympatric species.

Five seasonal groups have been recognized in odonates (Belyshev, 1963). *Coenagrion armatum* and *C. lunulatum* belong to the spring group, in which imagoes emerge in May and fly at most until July 20, and *C. pulchellum* belongs to the spring–summer group, in which imagoes emerge in early June and fly until late July or sometimes early August. The occurrence of these species in natural habitats is strongly overlapped in time (1.3 months). During the second 10 days of May, *C. armatum* is the first to fly, followed in about a week by *C. lunulatum* and then in the first days of June also by *C. pulchellum*. The first two species stop flying almost simultaneously, around mid-July; *C. pulchellum* flies for 2–3 more weeks.

Therefore, part of the flying period in two of the three species coincides with that of only one other species, *C. armatum* or *C. pulchellum*, while the remaining part coincides in all the three species. This peculiarity of flying in *C. armatum* and *C. pulchellum* should somehow manifest itself in the relative cyclicities of their abundance, as discussed below. *Coenagrion lunulatum* almost always flies simultaneously with the other two species. Hence, it can be suggested that *C. lunulatum* should have a cyclicity characterized by peaks of abundance that do not coincide with those of the other two species. *Coenagrion pulchellum* less often

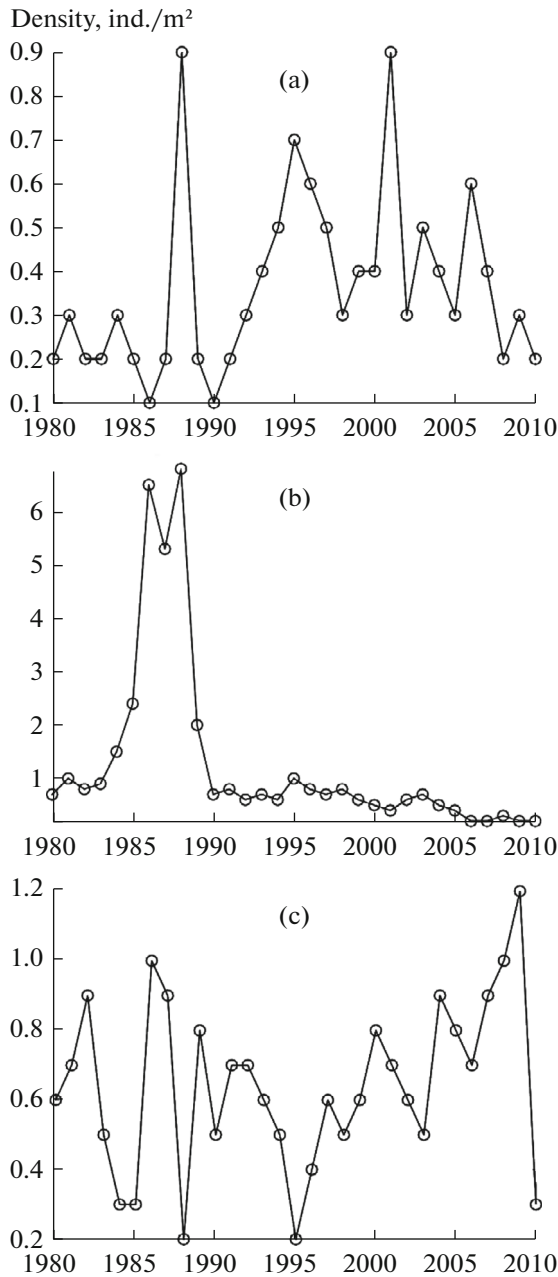
overlaps in space with *C. armatum* than with *C. lunulatum*, because the latter species is eurytopic, as shown by the censuses. The relatively low abundance of *C. armatum* in most years probably prevents this ubiquitous odonate from becoming a strong competitor for space of the two other species.

Consequently, a priori more stressed relationship should be established between *C. armatum* and *C. lunulatum*, which show a considerable overlap both in the time of flying and in biotopic preferences, than between *C. lunulatum* and *C. pulchellum* or between *C. armatum* and *C. pulchellum*, in which this overlap is less apparent. Using different methodological approaches, we shall try to explain how stress in the relationships of different pairs is relieved and eventually try to answer the question of how these taxonomically and ecologically close species coexist in a rather friendly manner in almost the same space and time.

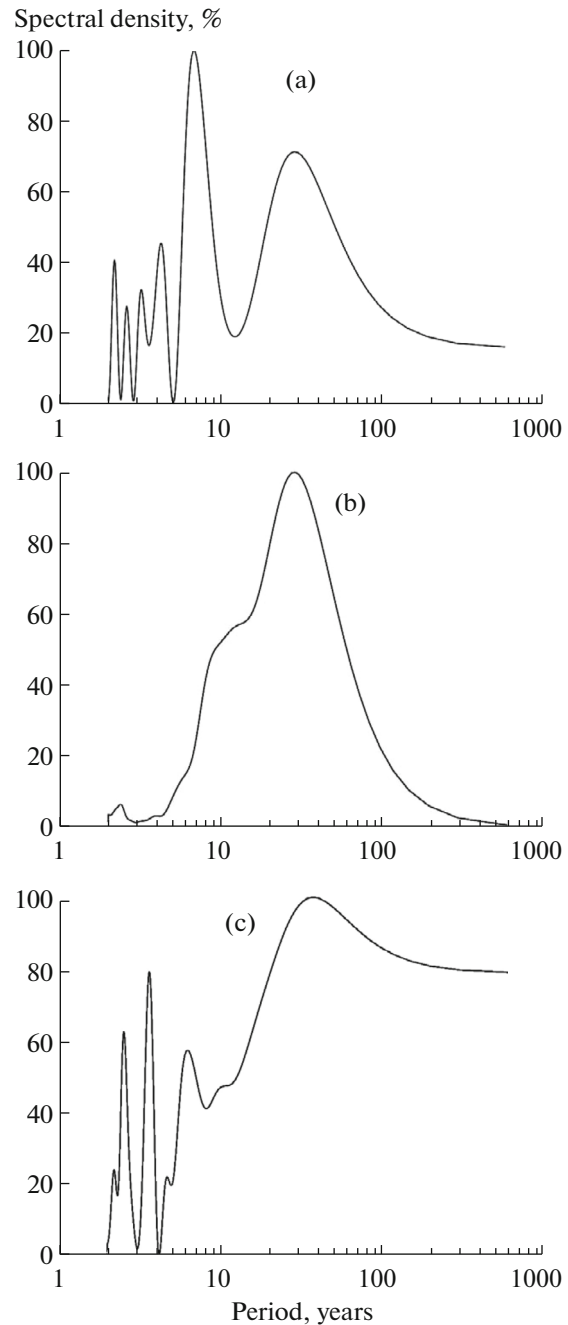
Changes in the abundance of these species on a long time scale (chronograms) appear as complex curves with many peaks and troughs (Fig. 1). Their abundance changed every year, and data on its average values over the long period of observations are as follows: *C. lunulatum* ( $1.27 \pm 0.62$  ind./m<sup>2</sup>) is the most abundant species, *C. pulchellum* ( $0.64 \pm 0.08$ ) is half as abundant, and *C. armatum* ( $0.36 \pm 0.08$ ) is 3.5 times less abundant; the differences between all these values are significant ( $t \leq 1.7$ ,  $p \leq 0.05$ ). Chronograms also show that in some years any of the three species could dominate in abundance. Thus, in 2008–2009 *C. pulchellum* was twice as abundant as the other two species together (Fig. 1c). Calculation of correlation coefficients between population dynamics in different pairs of species yielded no significant values; in other words, the species showed no synchronicity in this parameter. Only some peaks, as well as troughs, coincided over the entire study period in the pairs *C. lunulatum*–*C. armatum* ( $r = 0.03$ ) and *C. lunulatum*–*C. pulchellum* ( $r = -0.06$ ); in the pair *C. armatum*–*C. pulchellum* ( $r = -0.34$ , a value close to significant) many peaks and troughs were in antiphase: one population was growing while the other was declining, which presumably alleviated competition between them.

To learn more about cyclicity, the distances between peaks in chronograms are usually estimated, thereby gaining a visual idea of possible cycles in the population dynamics of animals. The longest cycle in *C. armatum* has a 15-year period, but 8- and 4-year cycles are also possible in this species; *C. lunulatum* has a 9-year cycle, but no other possible rhythms can be visualized from the chronogram; finally, *C. pulchellum* has a cycle with a period of over 24 years and also a distinct 4–5-year cycle. These data on population cyclicity can hardly be considered sufficient, although in the early 20th century most cycles were determined by this particular method (Formozov, 1935).

To improve the picture of cyclicity, let us represent our data on a frequency scale rather than on a time



**Fig. 1.** Chronograms of long-term population dynamics in odonates of the genus *Coenagrion*: (a) *C. armatum*; (b) *C. lunulatum*; (c) *C. pulchellum*.



**Fig. 2.** Spectra of long-term rhythms in the population dynamics of odonates of the genus *Coenagrion*: (a) *C. armatum*; (b) *C. lunulatum*; (c) *C. pulchellum*.

scale. Although losing information on fluctuations in abundance, we thus will acquire precise data on hidden periodical components of our chronograms and on relative powers of these cycles.

We have drawn frequency spectra for population dynamics of each of the three species (Fig. 2) and calculated the cycles and their powers (Table 2). We have found some similarity in these spectra by comparing the periodicity of the respective cycles. Thus, all spec-

tra include similar large cycles (28- to 35-year) in the low-frequency band. These cyclicities allow populations to synchronize their population rhythm to the “Brickner cycle” described more than once (Shnitnikov, 1957; Druzhinin, 1987; Taranyuk, 2000). All spectra also include similar small cycles (2.2- to 2.6-year) in the high-frequency band of the spectrum. Similar cycles in the medium-frequency band of the spectrum (3.2- to 6.7-year) are traceable only in two

**Table 2.** Values of harmonic components of long-term dynamics in populations of three odonate species

Species	Period, years					
	25.0–35.0	7.0–5.0	4.9–4.1	4.0–3.0	2.9–2.5	2.4–2.0
<i>C. armatum</i>	$\frac{29.5^*}{0.22^{**}}$	$\frac{6.7}{0.28}$	$\frac{4.2}{0.12}$	$\frac{3.2}{0.09}$	$\frac{2.6}{0.08}$	$\frac{2.2}{0.12}$
<i>C. lunulatum</i>	$\frac{28.0}{21.40}$	–	–	–	–	$\frac{2.4}{1.40}$
<i>C. pulchellum</i>	$\frac{35.0}{0.22}$	$\frac{6.2}{0.13}$	$\frac{4.6}{0.05}$	$\frac{3.6}{0.17}$	$\frac{2.5}{0.14}$	–

\* Period (years); \*\* power (measured in units of spectral density).

spectra, those of *C. armatum* and *C. pulchellum*. Subsequent analysis of the rhythms using their powers showed that the similarity between spectra is relative: almost every cycle has its own specific power.

As suggested earlier, the population dynamics of *C. lunulatum* is visibly different in cyclicity from those of the other two species. It includes only two distinct harmonic components, the high- and low-frequency cycles, with the low-frequency cycle being determinative. The population dynamics of *C. lunulatum* is more similar in cyclicity to that of *C. armatum*, but the abundance of the former species is on average twice as great. If periods in population dynamics are similar, the stress of competition between species is relieved through differences in power between corresponding periodical components. The cyclicities of *C. lunulatum* and *C. pulchellum* coincide only in the Brickner cycle. In this case, high abundance of *C. lunulatum* corresponds to relatively low abundance of *C. pulchellum*: the difference reaches or exceeds an order of magnitude.

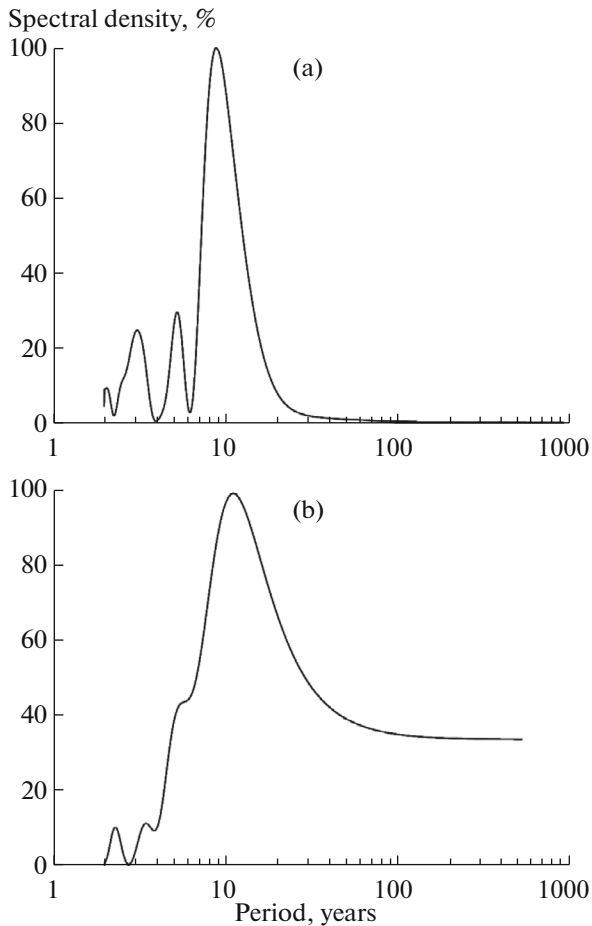
The suggestion about the peculiarity of cyclicities found in *C. armatum* and *C. pulchellum* has been confirmed. They are similar in periods, but the relative powers of the periodical components within each frequency band are different. Thus, the Brickner cycle and approximately 7-year cycle are almost equally important for *C. armatum*, whereas for *C. pulchellum* the Brickner cycle is obviously more important: its power is twice as high as that of the 6-year cycle. The periodical components in the high-frequency band of the studied species are very similar in magnitude. Their power is relatively low and varies depending on species.

The diverse relationships between periodical components in the population dynamics of the studied species can be explained by their specific ecological features described above. Thus, each species has its own biotopic preferences, which decrease the need for distinct differentiation in time; this is clear from the considerable overlap between the spectra of the two species. On the other hand, both species have been found in almost all studied biotopes in the same periods of time. In this case the species are well differentiated temporally due to asynchronicity of the highest

peaks of abundance. Their powerful low-frequency cycles occupy different frequency bands in the spectra, giving the less abundant population of *C. armatum* a chance to alleviate the interaction with the population of *C. pulchellum*: abundance reaches a peak every 7 years in the former and every 35 years in the latter species. In addition, the abundance of *C. pulchellum* visibly increases every 3.6 years, which is also asynchronous with the peaks of *C. armatum*.

All these cycles can be stable in habitats only in the presence of natural cyclicities with a similar period, and such cyclicities are, indeed, known. Thus, long-term variations of temperature are cyclic: the most common cycles have a period of 2–4, 5–6, or 7–9 years (Korotina, 2002). Natural cyclicity of humidity with a period of 3–6 years is also common (Fefelov, 1999). In addition, approximately 7-year georhythms of the Earth have been described (Yakushev, 2002), as well as 5–7-year cycles of winter severity (Byalko and Gamburgtsev, 2000). All these reliable synchronizers allow odonates to maintain the stability of long-term rhythms. Some of them (winter severity, temperature cycles) not only serve as agents prolonging the rhythms but are also important for adaptation of species. Since the severity of winters is cyclic, the depth of freezing of water bodies is also cyclic, particularly in shallow areas, which can be a very important factor for larval development. The most common high-frequency natural rhythm has a period of 2–3 years. It manifests itself in changes of temperature and humidity; the same period is typical of crop yields in Novosibirsk oblast (Efimov et al., 1983). No wonder that such cyclicity is also typical of all three studied odonate species.

Odonates are amphibiotic insects, and the water regime of the area they inhabit is an environmental factor of primary importance for them. Their abundance directly depends on water level and decreases as this level drops. As the water level rises, the number of temporary water bodies increases and environmental conditions for odonate larvae are improved: oxygen deficiency in summer and in winter becomes less acute, and the extent of drying and freezing decreases. Lake Chany is a good indicator of water transgression and regression in the study area. The littoral zone of



**Fig. 3.** Spectra of natural rhythms for Lake Chany: (a) water balance, (b) water level regime.

the lake is occupied by dense reed beds extending for several hundreds of meters from the shore, which are covered with water in years corresponding to the transgression phase. The latest regression phase in the Baraba forest–steppe (including the Chany test area) started in 2003, and the reed zone almost dried up by 2008–2012. It is expected that a new transgression phase will start in 2014–2015, following the 11-year cycle known as “Baraba natural cycle” (Maksimov

et al., 1979; *Prirodnye...*, 1982; *Ekologiya...*, 1986). Other cycles associated with Lake Chany are also known; their periods are 40–45, 20–22, and 6 years (*Pul'siruyushshee...*, 1982; Savkin et al., 2005).

Thus, it appears that changing parameters of Lake Chany are the strongest natural factor synchronizing the cyclicality of odonate populations in the Baraba forest–steppe. It has already been shown that the abundance of the dragonfly *Libellula quadrimaculata* L., 1758 is positively correlated with the water balance of the lake (Popova and Kharitonov, 2010). It is noteworthy that the hydrological parameters of Lake Chany are influenced by human activities, which have become increasingly intensive since the early 18th century; as a result, the lake surface area has decreased from 10000–12000 to 2000–4000 km<sup>2</sup> (*Pul'siruyushshee...*, 1982). Such an indirect influence of the anthropogenic factor has also been revealed in the Southern Urals: long-term changes in the structure of the odonate taxocenosis proved to be strongly associated with the growing network of artificial water bodies; this association is determined by the biology of odonate development (Popova and Haritonov, 2008).

We also analyzed hydrological parameters of Lake Chany such as the water level regime and water balance. First of all, we analyzed linear correlation between changes in these parameters and fluctuations in the abundance of the studied species over a similar period of 31 years; none of the coefficients were significant. Then we determined the cyclicities of these natural processes (Fig. 3) and compared them to the rhythms of population dynamics. The water balance and level regime of the lake over the study period have a maximum cyclicality of 9 and 11.4 years, respectively (Table 3), and a minimum cyclicality of 2–4 years. The 9-year water balance cycle and 11.4-year cycle of water level in the lake, roughly corresponding to the “Baraba cycle,” are the most powerful. However, no such periodical component has been found in the population cycles of the studied odonate species. The 5.3-year water balance cycle and 7.6-year cycle of water level in the lake are less powerful but clearly pronounced in the spectra. Similar rhythms are found in the cyclicities of *C. armatum* and *C. pulchellum*, which makes it possible to use some of them (the 6–7-year ones) as

**Table 3.** Cyclicity of hydrological parameters of Lake Chany

Parameter	Period, years					
	30.0–50.0	9.0–10.0	9.0–5.0	4.9–4.1	4.0–3.5	2.4–2.0
Water level	–	$\frac{11.4^*}{192^{**}}$	$\frac{7.6}{37}$	–	$\frac{3.5}{21}$	$\frac{2.3}{19}$
Water balance	–	$\frac{9.0}{328}$	$\frac{5.3}{97}$	–	$\frac{3.1}{80}$	$\frac{2.1}{30}$
Water level (from Savkin et al., 2005)	40.0–42.0	12.5	9.0	6.0	3.0	–

\* Period (years); \*\* power (measured in units of spectral density).

reliable indicators of time. Long-term cyclicity of *C. lunulatum* is associated with the Brickner cycle. High-frequency (2–4-year) cycles, which precisely correspond to the low-power high-frequency cycles of all three studied species, proved to be the least powerful of all natural cycles analyzed (Tables 2, 3). Similar cyclicity is found in the constant 2–3-year natural summer rhythm, which manifests itself in changes of temperature and humidity.

## CONCLUSIONS

The chronograms of long-term population dynamics of abundance for the studied odonate species are complex curves with numerous peaks and troughs. These curves have provided little information: comparison of abundance levels by years and very approximate idea of the cycles that are possible in these species. The calculated pairwise correlation coefficients between population dynamics of different species lack statistical significance, indicating there is no synchronicity by this parameter.

Therefore, classical chronograms and correlation coefficients have revealed only the most general patterns of changes in population size, providing no insight into species-specific features of the population dynamics. Such an insight could be gained by means of spectral analysis, which has revealed periodical components in the population dynamics of each species. These population cyclicities (spectra) proved to be convenient biological parameters that expose the essence of long-term patterns of population dynamics of abundance.

The periods of the cycles range from about 30 years in the “Brickner cycle” to 2–3 years. Despite taxonomic proximity of the studied species, their spectra are clearly distinguishable. Each species is characterized by specific long-term cycles of population dynamics in the low-frequency band of the spectrum: about 30 years in *Coenagrion armatum*, 28 years in *C. lunulatum*, and 35 years in *C. pulchellum*. In cases where the cycles are similar (in the high-frequency band of the spectrum), the spectra of different species differ in relative power. Differences between spectra should alleviate the stress of competition. In addition, they provide evidence for separation in time between species that have generally similar ecological standards.

An important condition for the maintenance of population fluctuations is their synchronization with external cyclic processes that have similar periods: in such a case, fluctuations are not damped and serve as adaptations of the population to changes in environmental conditions. Our calculations have shown that many cycles in the dynamics of the studied odonate populations in their habitats include cyclic processes similar in periodicity: fluctuations of climatic parameters (2–3 year cycles for all three species) and fluctuations of hydrological param-

eters in Lake Chany (2–4 year cycles for all three species and 6–7 year cycles only for *C. armatum* and *C. pulchellum*), which largely determine general water supply to the study area. These particular natural rhythms can be used as external indicators of time for the studied species of the genus *Coenagrion*. All rhythms in the range of 2 to 4.5 years are almost equal in values and almost coincide with high-frequency oscillations of hydrological parameters of Lake Chany in whose basin these populations live; in other words, these fluctuations of abundance make all these populations adapted to local and regular changes that are important for them.

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