ISSN 1995-4255, Contemporary Problems of Ecology, 2018, Vol. 11, No. 6, pp. 551–562. © Pleiades Publishing, Ltd., 2018.
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Cyclicity of Long-Term Population Dynamics in Dragonflies of the Genus *Sympetrum* (Odonata, Anisoptera) in the Basin of Lake Chany

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Received March 7, 2018; in final form, April 12, 2018

Abstract—This work is directed at continuous studies of cyclicity of long-term (1980–2010) population dynamics of odonates in the basin of Lake Chany (in the south of Western Siberia). Four sympatric species of the genus *Sympetrum* have been investigated by spectral analysis method. The cycle spectra of population dynamics have been constructed for each species; the basic parameters of these cycles (period, phase, and power) have been calculated. Special number cycles have been found for each species. Interspecies differences increased in the direction from high to low frequencies of the spectrum. In the cases of similar cycles, interspecies differences have been shown in the ratio of cycle powers and/or phases: identical phases can indicate the ability of species to increase their number synchronously with any of close species; different phases can indicate the possibility of a small-numbered species to reach its maximum number against the minimum number of numerous species. A comparison of sympatric species spectra of the genera *Coenagrion* and *Sympetrum* has led to the conclusion that, the more similarity there is in environmental standards among species inside a genus (as for *Sympetrum*), the more specific the species frequency spectra are. All species of the genus *Sympetrum* can synchronize their number fluctuations with 2- to 3 and 4- to 5-year fluctuations of the local climate. Also specific synchronization with important nature-climatic rhythms was found for each species: for *S. danae*, with an 18-year rhythm of the level of Lake Chany and with a 16-year rhythm of June temperatures; for *S. flaveolum,* with a 24-year Brickner cycle, with an 8-year cycle of rainfall, and with a 28-year cycle of April and May temperatures; for *S. vulgatum,* with a 40- to 42-year cycle of the level of Lake Chany, with 12-year cycle of rainfall, and with a 7-year cycle of April and June temperatures; and for *S. sanguineum*, with a 7-year cycle of April and June temperatures. Perhaps the adaptation mechanism of species to each other and to environments is enclosed in the cyclicity of long-term fluctuations of species number.

Keywords: Odonata, *Sympetrum* spp., long-term population dynamics, population cycles, spectral analysis, Western Siberia, Lake Chany basin, Barabinsk forest steppe

DOI: 10.1134/S1995425518060082

INTRODUCTION

The number dynamics are directly or indirectly associated with environmental factors (abiotic and biotic), as well as with processes that spontaneously take place within the population itself (Bigon et al., 1989; Sinclair, 1973; Symonides, 1979). The variability of the population size can be considered an adaptive response to the existence conditions of the species (Nikol'skii, 1965). Insect populations are also subject to number fluctuations (Varley and Gradwell, 1968; Harcourt, 1971; Poole, 1974).

Odonates, as amphibious insects, have water (egg and larval) and terrestrial (imaginal) development stages in their life cycles. With such a complex life cycle, it is very difficult to isolate the factors affecting the number of the local population of odonates (Corbet, 1999; Stoks and Córdoba-Aguilar, 2012). Only abiotic factors universal for all odonates could be emphasized: climate (Popova, 2001a; Hickling et al., 2005; Hassall and Thompson, 2008; *Monitoring climatic*..., 2010) and weather conditions (Belyshev et al., 1989; Dingemanse and Kalkman, 2008; Suhling et al., 2015). All phases of the odonate life cycle are closely related. Thus, quantitative and qualitative parameters of egg laying determine larval development (Hottenbacher and Koch, 2006; Remsburg, 2011). The conditions and characteristics of aquatic larvae development affect the life of terrestrial imago, for example, their number (Popova, 2010; Popova and Haritonov, 2010; McCoy et al., 2009; Stoks et al., 2005) and dispersal capacity (Conrad et al., 2002; Benard and McCauley, 2008; Haritonov and Popova, 2011). In foreign environmental literature, such an indirect link

† Deceased.

between the aquatic and terrestrial components of the taxocene is called carry-over effects (McPeek and Peckarsky, 1998).

The study of larval populations of different odonate species revealed many factors determining their numbers. These factors include the properties of the reservoir, both hydrological (Popova, 2001, 2010) and biotopical (Popova and Smirnova, 2010; Popova and Haritonov, 2014a), and food resources (Corbet, 1999; McPeek, 2008; Sahlén et al., 2008). Biotic interactions are also important. They include territorial intra- and interspecific competition (Ryazanova, 1998; Dronzikova, 2010; Pierce and Crowley, 1985), as well as the stress susceptibility and mortality of larvae caused by interaction with predators (McPeek and Peckarsky, 1998; Baker et al., 1999; Stoks et al., 2005; Katayama, 2013) and parasites (Serbina and Haritonov, 2001; Baker et al., 2007; Wildermuth and Martens, 2007). Our field experience with adult odonates, as well as literature data (Belyshev et al., 1989; Haritonov, 1991; Corbet, 1999; Conrad et al., 2002; Remsburg and Turner, 2009; Harabiš and Dolný, 2010; Remsburg, 2011), suggest that all the factors listed above for larvae are relevant for adults, only with the difference that adults have terrestrial biotopes instead of water ones. In addition to these factors, the already-mentioned larval heritage also influences the number characteristics of the odonate adult population. As a result, the number of imago odonates, consisting of different components, is a complex; integrated; and, accordingly, very informative population indicator, especially in its temporal dynamics. One adequate characteristic of the temporal organization of the biological system is the spectrum of its periods, or cycles (Martynyuk et al., 2007).

Cycles of population dynamics have been described for many populations of animals; their characteristics have been determined (Chernyavskii and Lazutkin, 2004; Duvanova et al., 2009; Erdakov, 2011; Kiselev and Yamborko, 2014; Telepnev and Erdakov, 2014; Bjørnstad et al., 1998; etc.). We did not know any publications on odonate cycling. We have previously investigated the long-term cyclicity of population variations in several species of damselflies (suborder Zygoptera) of the genus *Coenagrion* in Lake Chany basin (Popova et al., 2016a). In the present work, we examined dragonflies (suborder Anisoptera) of the genus *Sympetrum* inhabiting the same territory and in the same multiyear sampling as *Coenagrion* spp. Representatives of the genus *Sympetrum* play an important role in biocenosis of the temperate belt due to their high numbers and specific ecological features (Sukhacheva et al., 1988; Popova, 1999; Popova and Haritonov, 2014b; Corbet, 1999).

We chose the objects according to their following characteristics: (1) close relation (the species belong to the same genus), (2) sympatricity (species inhabit the investigated territory), and (3) relative stability of abundance (throughout the time of observation, the species more or less retained their number category). With all their close relations, these species coexist quite amicably in practically the same space and time.

The aim of this study is to reveal the regularities of the cyclicity of the multiyear course of abundance of four species of the genus *Sympetrum*.

The research tasks are as follows: construct the spectrum of population rhythms, calculate the periods and powers of the harmonic components (cycles or rhythms) in the dynamic spectrum of each species, analyze chronograms and spectra taking into account the ecological features of the species, and elucidate natural time sensors that support the rhythms of the odonate number.

In order to avoid overloading the text with frequently recurring Latin, we found it possible to use the Latin name of the genus *Sympetrum*, sympetrum, already adopted by odonatologists and, accordingly, to call the odonates of this genus "sympetrums."

METHODS AND MATERIALS

Research Site

The investigations were carried out in the southeast of Western Siberia, in the Barabinsk forest steppe, in the basin of Lake Chany. The research site (54°32′–54°39′ N, 78°06′–78°19′ E) is located in Novosibirsk oblast.

Study Object and Its Ecological Characteristics

Four sympatric species of odonates of the genus *Sympetrum* Newman, 1833: *S. danae* (Sulzer, 1776), *S. flaveolum* (Linnaeus, 1758), *S. sanguineum* (Müller, 1764), and *S. vulgatum* (Linnaeus, 1758) were studied. These species have wide ranges: three are trans-Eurasian (*Sympetrum flaveolum*, *S. sanguineum*, and *S. vulgatum*) and one is circumboreal (*S. danae*). Odonates are of medium size: wingspan is 50–60 mm, length of the rear wing is 25–40 mm, and body length, 30–50 mm. The largest species of these four is *S. vulgatum* and the smallest is *S. danae*. Due to the large intraspecific variabilities, the dimensional characteristics of all species overlap quite well. In the temperate zone, the sympetrums belong to the summer–autumn phenological group. The flight time for these species coincides: from the middle of June to the beginning of October.

Topical preferences of the species can be traced: *S. flaveolum* and, especially, *S. sanguineum* are *woodside* species, preferring ecotones on the border of arboreal and shrubby vegetation and open spaces; *S. vulgatum* is a *steppe* species, inclined to open biotopes; and *S. danae* is a *forest* one, associated with tree and shrub vegetation (Popova, 1999). The larvae have a fairly similar set of requirements: they develop in semiflow and stagnant water bodies with abundant

Table 1. Statistical characteristics of the average number (ind./m^2) of odonates of the genus *Sympetrum*

Species	*n*, years	min–max	$M \pm m$	σ	*CV*	Trend
Sympetrum danae	31	0.5–2.1	1.19 ± 0.07	0.41	34.45	1.300–0.007* t NS
Sympetrum flaveolum	31	0.3–3.2	1.56 ± 0.14	0.76	48.72	1.599–0.003* t NS
Sympetrum sanguineum	31	0.02–0.44	0.17 ± 0.02	0.11	64.71	0.256–0.006* t R2 = 0.241; α = 0.05
Sympetrum vulgatum	31	0.3–3.2	1.31 ± 0.10	0.53	40.46	1.536 – 0.015* t NS

aquatic vegetation and the presence of a muddy bottom (Popova, 2001b).

The emerging odonates are widely dispersed from water bodies to terrestrial biotopes, where they actively feed for 2–3 weeks (from 7:00–8:00 a.m. to evening twilight). Imagoes and larvae hunt in all stories of the biocenosis and feed on a wide variety of animal food (bugs, flies, small lepidopterans, dayflies, caddis flies, hymenoptera, and spiders) that they can physically get; cannibalism was noted.

Material and Methods of Odonate Imago Sampling

A chronoecological analysis was based on the data of A.Yu. Haritonov and O.N. Popova on the number of odonate imagoes over 31 years (1980–2010). During this period, 16721 quantitative censuses were carried out; 614120 odonate imagoes were registered, including 120310 imagoes of sympetrums. The sampling were conducted annually and throughout the entire flight period of odonates, from May to October. The data for calculating density (ind./m^2) were obtained mainly by two methods: the mass capture–mark–recapture method and visual records on belt transects. A detailed description of the methods was previously published (Popova et al., 2016b).

To determine the number and characteristics of the harmonic components of Lake Chany (dynamics of the level and mirrors), we used the tabular data of long-term censuses (1971–2000) given in the work of V.M. Savkin et al. (2006). Data on precipitation and air temperature in the area of Lake Chany were taken from the same publication. Savkin et al. (2005) revealed the cycles of Lake Chany level changes on the material, which amounted to a series of 103 years, by "the classical spectral analysis method." We also included these data in our table (Table 4) of characteristic fluctuations of Lake Chany.

Analysis Methods of Sampling Data

The time series were presented in the form of chronograms; by spectral analysis we investigated the content of hidden harmonic components. The calculations were carried out using a package of spectral analysis programs owned by Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences (Novosibirsk). The *Harms* program by A.V. Tarnovskii was also used. The spectral density (power) was estimated by the Welch method (Marple, 1987); the most stable patterns of the spectral density distribution were selected. All calculations were performed using the free system for mathematical calculations GNU Octave (GNU...). For trends, the hypothesis of the difference of coefficients from zero was tested and the determination coefficient R2 was calculated. The statistical processing of the data was carried out with the help of Past software.

RESULTS

Throughout the study period, 1980–2010, the annual average number of species of the genus *Sympetrum* changed annually and in fairly wide ranges; its minimum value differed 4.2 times from the maximum for *S. danae*, 10.7 times for *S. flaveolum* and *S. vulgatum*, and in 22 times for *S. sanguineum* (Table 1). In decreasing order of average annual abundance, the species are located as follows: *S. flaveolum*, *S. vulgatum*, *S. danae,* and *S. sanguineum*. The first three species of this group had a fairly high population number; *S. sanguineum* was consistently small (Table 1). The mean differences (according to the Student's test) for all the listed species are significant ($t \geq 1.7$, $p \leq 0.05$), even for such close populations as *S. flaveolum* and *S. vulgatum* ($t = 1.8$).

The Spearman's rank correlation coefficient R_S was calculated to determine the synchronism of the evolution of the number of odonates (Table 2): the test for the sample distribution character in the series showed significant deviations from the normal distribution, so a rank criterion was used. Only one significant Spearman coefficient ($\alpha = 0.01$) was obtained.

Figure 1 shows chronograms reflecting the long-term changes in the number of species on the time scale. They look like complex curves with numerous peaks and drops.

Table 2. Spearman's rank correlations coefficient for odonates of the genus *Sympetrum*

Species	*S. danae*	*S. flaveolum*	*S. sanguineum*	*S. vulgatum*
S. danae	0			
S. flaveolum	–0.1729	0		
S. sanguineum	0.47627	–0.27318	0	
S. vulgatum	0.32103	0.33411	0.18554	0

Table 3. Characteristics of the cycles of long-term population dynamics in four species of the genus *Sympetrum*

Species	Period, years								
	20.0–30.0	10.0–19.0	7.0–9.0	5.1–6.0	4.1–5.0	3.6–4.0	2.9–3.5	2.5–2.8	2.0–2.4
S. danae	–	18.6*/0.097**	7.2/0.288	5.3/0.326	4.1/0.204	–	3.2/0.139	2.5/0.126 2.8/0.119	2.1/0.209 2.3/0.117
S. flaveolum	24.4/0.640	–	8.1/0.549	5.9/0.334	–	4.0/0.353	2.9/0.323	2.5/0.248	2.2/0.171
S. sanguineum	–	–	7.6/0.083	5.4/0.036	4.4/0.025	3.8/0.010	3.3/0.040 2.9/0.015	2.6/0.031	2.2/0.015 2.3/0.015
S. vulgatum	35.3/0.166	12.5/0.378	7.0/0.190	5.4/0.371	–	3.9/0.146	3.2/0.136	2.8/0.232	2.4/0.182 2.1/0.169

* Period (years); ** power (amplitude).

Using a fast Fourier transform, oscillation spectra were constructed for each species in several frequency bands: high, medium, and low (Fig. 2). The duration of our observations does not allow us to obtain a line spectrum of oscillations, only a continuous one. Cyclicity can be estimated on it as a peak in a certain frequency band. The more exponential a form of such a peak is and narrower its base is, the more accurately its period is determined in the spectrum image. What the spectra of all sympetrums have in common is a very broad base of the low-frequency peak, which can be explained by the insufficiently long interval of observations (31 years). Table 3 shows the results of calculating the periods and power cycles in the dynamics of each species; Table 4 shows the main parameters of the cyclicity of some natural and climatic factors in the habitat of odonates.

DISCUSSION

There are two common features in the picture of the dynamics of the sympetrum numbers: (1) despite the annual changes in population density, annual multiyear estimates of abundance are very stable and none of the species showed any outbursts or significant depressions throughout the observation period; (2) there was a gradual decrease in the number of species in the 31-year series of observations, especially for *S. sanguineum* (Table 1).

It is difficult to explain the dynamics of the number of species on the basis of a visual comparison of the chronograms: some peaks/recessions of the number coincided in these years; at the same time, often with the background of abundance decline of one species, a rise of the other was observed (Fig. 1). The calculation of the Spearman's rank correlation coefficient (R_S) reliably revealed synchronism of population fluctuation only for *S. danae* and *S. sanguineum* species ($R_S = 0.48$). This can be interpreted as the absence of tension between their populations: these species have different topical preferences, which should soften competition for common food resources and roosts. It is possible to assume antiphase ($R_S = -0.27$) in the dynamics of *S. flaveolum* and *S. sanguineum*, since this pair, having the same topical preferences, should strive to avoid competitive tension, separating their maximum perennial number in time. Correlation coefficients (even significant) and chronograms give fragmentary information about the dynamics of population density. The presentation of the long-term course of numbers not on the time scale, but on the frequency scale, makes it possible to investigate the functional connections.

Analysis of Frequency Spectra of Fluctuations in the Number of Species of the Genus Sympetrum

The frequency spectra of the studied species population rhythms were analyzed with the involvement of their ecological features. The species spectra are externally noticeably different from each other both in terms of harmonic components (the abscissa axis) and in terms of their powers (ordinate axis) (Fig. 2). Let us consider all the frequency zones of the species spectra we have constructed: high, medium, and low ones.

High frequencies (2–4.5 years) on all species spectra are characterized by close values of periods, and the power of the peaks is small. The most powerful approximately 4-year cycle was observed in three species out of four, with the exception of *S. sanguineum* (Fig. 2c). That is, every 2, 3, and 4 years, species have a low or medium number and can easily disperse in space, occupying their biotopes (steppe, woodside, or forest). Considering the similar flight time, such low-power cycles are a good adaptation of the species to each other for a certain period of time (2–4.5 years).

At medium frequencies (5–10 years), interspecies differences become larger, as is indicated by the location and high power of the cycles. It seems that a cycle of about 5–7 years is important for all species, but its importance, judging by the power of this rhythm, is not the same. It dominates on the spectra of *S. danae* and *S. vulgatum* (Figs. 2a, 2d) and its power is insignificant for the other two species, *S. flaveolum* and *S. sanguineum* (Figs. 2b, 2c). According to the power for *S. flaveolum* and *S. sanguineum*, the cyclicity of about 8 years is much more important (Figs. 2b, 2c), and this cyclicity has the most powerful peak on the entire spectrum for *S. sanguineum*. However, in *S. danae* this rhythm also has a high power—a subdominant peak on the spectrum (Fig. 2a).

Despite the closeness of some cycles in different species, their phase relationships may differ. Therefore, for the shared 7-year cycle for the species, such differences lead to the fact that *S. danae* and *S. sanguineum* reach their maximum at the time when *S. flaveolum* and *S. vulgatum* are at their minimum. This phase differentiation has a certain biological meaning: *S. flaveolum* and *S. vulgatum* are the dominant species in this group (Table 1), so it is natural that other small species increase their numbers more easily with a decrease in the number of dominants.

Another example of phase relations: all four species have a cycle of 5.5 years, which for two species, *S. danae* and *S. vulgatum*, judging by its high power, is especially important (Figs. 2a, 2d). A comparison of the parameters of this cycle showed that the species *S. danae*, *S. vulgatum*, and *S. sanguineum* are in anti-

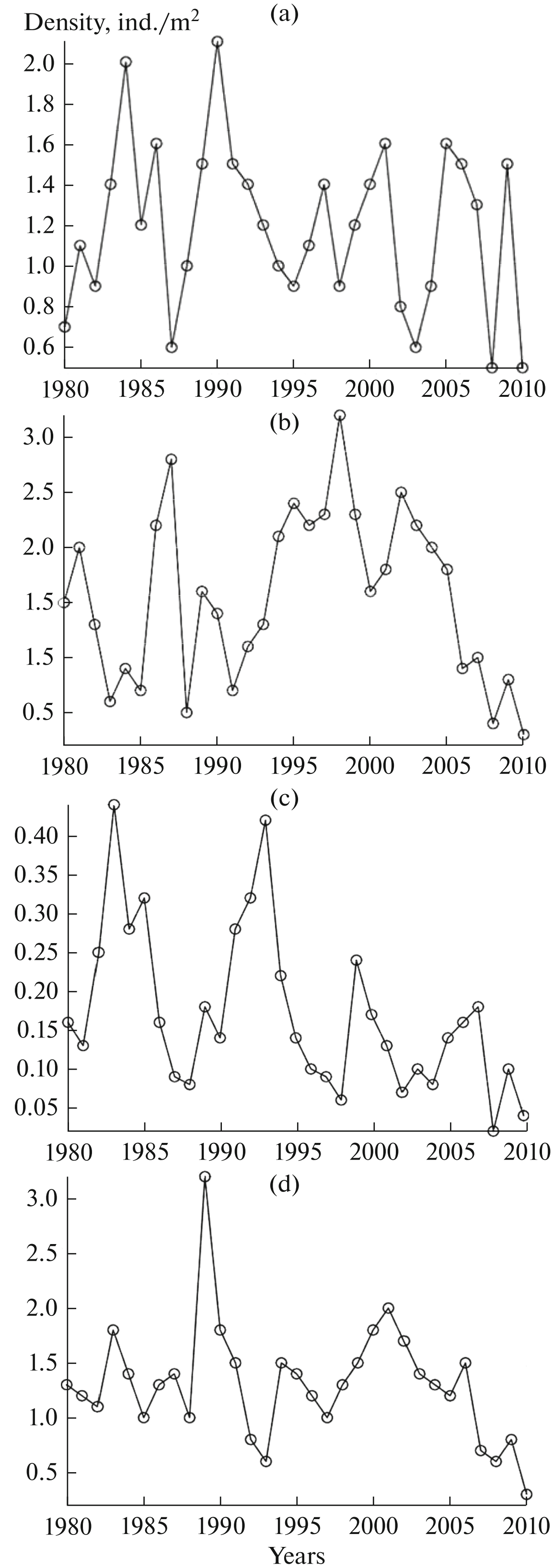

Fig. 1. Chronograms of long-term population dynamics in odonates of the genus *Sympetrum*: (a) *S. danae*, (b) *S. flaveolum*, (c) *S. sanguineum*, and (d) *S. vulgatum*.

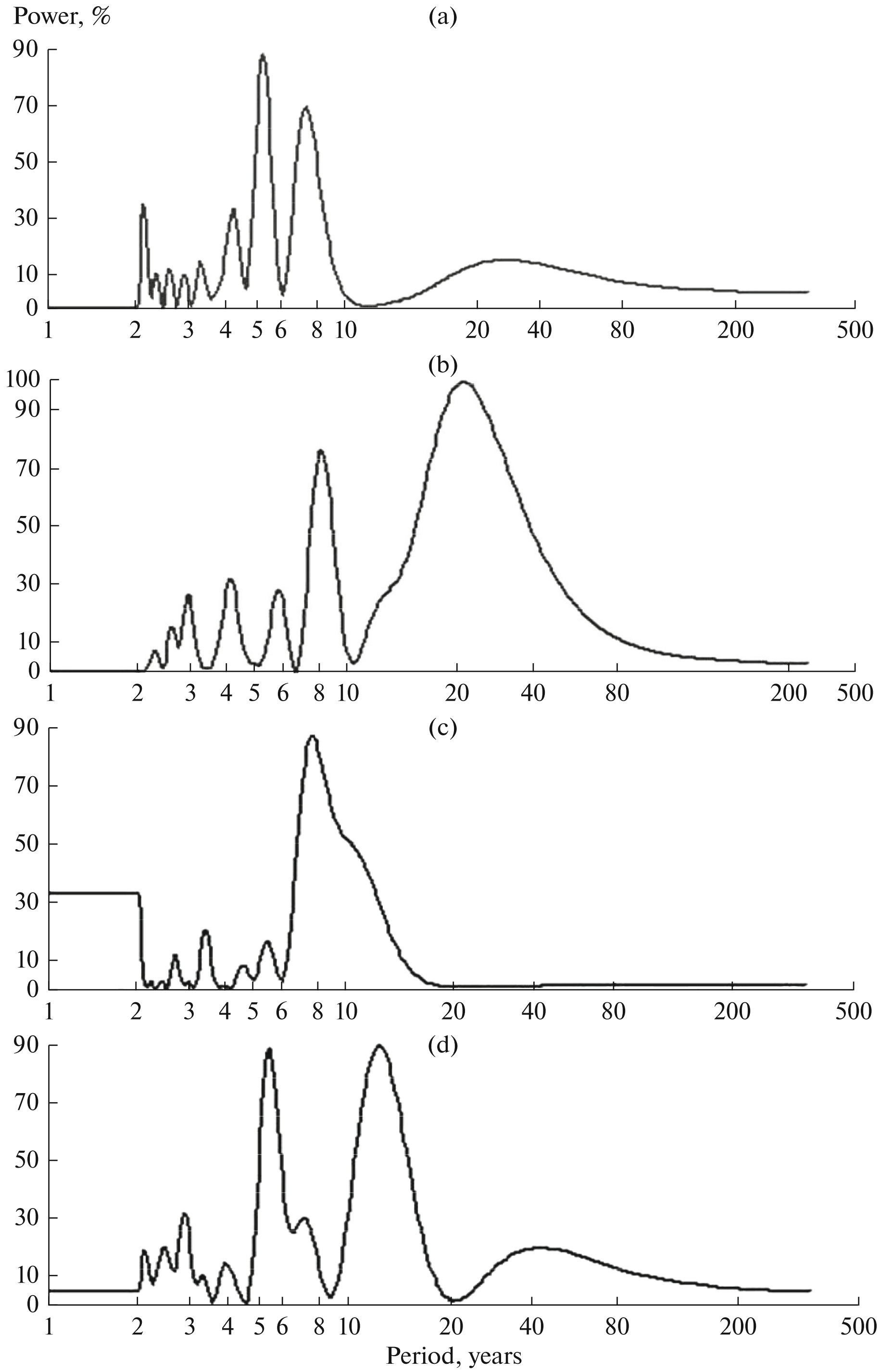

Fig. 2. Spectra of cycles of long-term population dynamics in odonates of the genus *Sympetrum*: (a) *S. danae*, (b) *S. flaveolum*, (c) *S. sanguineum*, and (d) *S. vulgatum*.

phase to the most numerous *S. flaveolum*: that is, every 5.5 years the maximum population density of the first three species is reached with a minimum population density of the fourth. This event may be important for maintaining the viability of populations of small- and average-number species *S. sanguineum* and *S. danae*, as well as for the separation in time of two numerous species, *S. flaveolum* and *S. vulgatum* (Table 1).

The greatest interspecific cycle differences were observed in the low-frequency zone (from 10 years and more): from the complete absence of harmonic constituents in *S. sanguineum* to the more than 30-year

Table 4. Cyclicity of some environmental and climatic factors in the habitat of odonates of the genus *Sympetrum*

Characteristic		Period, years								
		20.0–30.0	10.0–19.0	7.0–9.0	5.1–6.0	4.1–5.0	3.6–4.0	2.9–3.5	2.5–2.8	2.0–2.4
Level dynamics of Lake Chany		42.7*/13.24**	17.9/28.1 13.3/24.287 10.7/16.449	8.5/8.368 6.9/9.24	6.1/7.88 5.5/4.277	4.2/3.024 5.0/4.602	3.8/4.415	3.5/2.555	2.8/2.359	2.4/2.355
Mirror dynamics of Lake Chany		39.4/20.733	–	9.9/110.143	–	4.7/38.664	–	3.5/36.888	2.9/14.574 2.6/21.039	2.2/13.477
Precipitation		35.3/1.501	12.6/3.551	8.1/3.702	–	4.3/1.488	3.8/1.269	3.2/1.261	2.6/0.999	2.1/1.136
Temperature	April	28.0/29.6	–	7.1/18.8	–	4.7/53.1	3.6/15.1	–	2.8/27.5	2.1/2.9
	May	28.0/13.9	–	9.5/17.8	–	4.7/16.4	–	3.5/2.7	2.5/18.9	2.1/3.6
	June	–	16.0/43.3	7.1/26.9	–	4.3/22.1	–	3.4/25.9	2.9/31.1	2.0/26.4

* Period (years); ** power (amplituda).

cycle in *S. vulgatum*. A gradual increase in the period of the harmonic at low frequencies is observed successively in the series *S. danae*, *S. flaveolum*, and *S. vulgatum*; the power of this peak among them is different (Fig. 2).

In the above analysis of frequency spectra, we focused on the differences in the cyclicities of the species and reduction of interspecies competition for vital resources related to them. However, the sympetrums also have similar cycles with similar phases and powers. That is, the species are able for some time to increase their numbers synchronously with any of the closely related species, regardless of interspecies competition. Such plasticity, perhaps, could be explained by the ecological peculiarities of the sympetrums, connected with their biotopic distribution (the presence of preferences), reproduction, and nutrition. The investigated species of odonates are weakly related to the sites of their emergence and can lay eggs in a variety of water bodies, and sometimes even simply on the ground in relief depressions that will be filled with meltwaters in the spring. All these contribute to the presence of a large number of potential reproductive sites and, accordingly, decrease the competition for them, usually the hardest competition for the odonates. Odonates are omnivorous predators, so under normal living conditions they should not lack food. However, food reserves can vary greatly depending on the biotope, the season, the specific dynamics of the number of individual species of victims, weather, and other conditions. In addition, it was shown by serological analysis that some species show a selectivity of food objects: for example, butterflies in the diet of odonates were found only in the samples of *S. flaveolum* and *S. danae* species, and clegs were only in *S. vulgatum* (Sukhacheva (Smirnova), 1989). Therefore, in some years, with an excessive increase of population densities, competition between species can be strengthened, but in general their basic vital resources (food, territory, and reproductive sites) for sympetrums are almost always available.

Number dynamics spectra of the species of the genus *Sympetrum*, as well as earlier considered representatives of the genus *Coenagrion* (Popova et al., 2016a), have their own species specificity only with the amendment that these spectra in the sympetrums are more distinct and specific in comparison with narrow-winged damselflies: the species spectra of narrow-winged damselflies contain similar cycles in all three investigated frequency zones, while, in sympetrums, similar cycles are noted only in the zone of high and partly middle frequencies. Although in all cases the similarity of the cycles is relative, almost every cycle has its own power value. Species of the genus *Sympetrum*, as well as species of the genus *Coenagrion*, are closely related, inhabit the same territory, and have topical preferences. Nevertheless, sympetrums have certain circumstances that can strengthen interspecies competition, which probably have been reflected in the greater specificity of their species spectra. Therefore, sympetrums, being medium-sized odonates and active flyers, cannot be objectively related to a certain territory for a long time. They fly around and sit around a large territory, including biotopes of other species. Narrow-winged damselflies, having a small size and a weak flight, are more moderate in their movements, confined mainly to the preferred biotope. The almost complete coincidence of the flight dates of sympetrum species in comparison with narrow-winged damselflies should also be noted. Perhaps these two reasons—the strong overlapping of the niches and the dates of flight—lead to the fact that species of the genus *Sympetrum* have more clearly defined adaptive characters than those of the genus *Coenagrion*.

In general, according to their morphological structure, lifestyle, and environmental requirements, species of the genus *Sympetrum* are a relatively homogeneous group of animals with a functionally uniform role in the community (Popova, 1999). Such groups in environmental literature are termed *guild* (Pianka, 1981; Root, 1967). It is accepted to call a sympatric sum of different species populations of odonates an odonato-complex (Haritonov, 1994). The complex is not a random set of species. There are facts of high repeatability of species complexes even on very diverse water bodies. The following regularity was revealed for odonates of the genus *Sympetrum*: 4–5 species fly together in one local biotope, the number of dominants is no more than 3, and the structure of their dominance can vary (Popova, 2001c). We have noticed that the change in the structure of sympetrum dominance occurred in the years of the rise in the odonate number. It is approximately every 5th–7th year, which fits into the 5–6 and 7- to 8-year powerful cycles.

Perhaps one of the decisive factors of the complex formation is the effective separation of niches by sympatric species, which developed evolutionally as a result of competition (Reimers, 1994). At low population densities, species of the genus *Sympetrum* are distributed in space more or less locally, each in its preferred biotope and in its ecological niche (in accordance with the principle of competitive exclusion). At high densities, species go beyond their biotopes, thereby invading other ecological niches. This situation is consistent with the paradox of J. Hutchinson (for two or more species): species can coexist in the same ecological niche using the same resources. Considering the mosaic nature of the Barabinsk forest-steppe landscapes (the scrub meadows and forest outliers are closely intertwined), all four sympetrum species show a large overlap of their niches, forming a single great ecological niche, the *superniche*, in which the total maximum density of populations can reach 25 ind./m^2 (Popova, 2001c).

Natural Time Sensors

For the stable (continuous) rhythm of an endogenous population, it is necessary to synchronize it with an external similar rhythm (Erdakov, 1991; Kausrud et al., 2008; Korpela et al., 2013; etc.). We compared the cycles of odonates (Table 3) with some natural and climatic rhythms of their habitat (Table 4): the level and the mirror of Lake Chany and precipitation and air temperature. These parameters were taken in accordance of their importance for the odonates (Belyshev et al., 1989).

As amphibious insects, an aquatic environment is of particular importance for odonates. In temperate latitudes, the main part of odonate life cycle (1–3 years) is in water preimaginal phases, while the flight of adults occurs in the most favorable and shorter summer season. The density of the larval populations, and ultimately the imaginal populations, is directly related to the water regime of the territory. During the rise in the water level, the number of water bodies increases and the conditions of larval development improve: the summer and winter deficiency of oxygen decreases, as does the scale of their drying and freezing. This, in turn, leads to an increase in the number of habitats and survival of the larvae, resulting in an increase in the number of populations of odonates. Conversely, the number of odonates decreases in the period of low water content on the territory. A clear indicator of manifestation of the humidification transgressive–regressive phases of the territory is Lake Chany, the so-called pulsating lake, which has several cycles of water-level fluctuations: the maximum one is about 100 years, the minimum is 2–4 years, and there are several intermediate ones (*Ekologiya*..., 1986). For example, we determined that the number of populations of *Libellula quadrimaculata* L., 1758 is strongly dependent on the water balance of Lake Chany (Popova and Haritonov, 2010) and is maximum 1 to 2 years after reaching the maximum water level.

In the high frequency zone, all studied species of odonates have pronounced cycles of abundance (Table 3). In the same frequency zone, all the analyzed natural and climatic factors also have stable and power conspicuous rhythms (Table 4). Perhaps the cycles of odonates in the range of 2–4.5 years are adapted well to the dynamics of local conditions.

In the midfrequency zone, the species spectra of rhythms begin to differentiate (Tables 3, 4). Species *S. danae* can fit to the 4- to 6-year cycle of the level and mirror of Lake Chany, *S. flaveolum* can fit to the similar 8-year cycle of precipitation, and *S. vulgatum* can fit to the 5- to 7-year cycle of the level of Lake Chany and to the 7-year cycle of April and June temperatures. *S. sanguineum*, having intermediate values of periods, can fit its cycles almost simultaneously to different natural rhythms in the range from 4 to 7 years.

Significant differences in adaptations to natural cyclicity were observed in the low-frequency zone.

So, *S. vulgatum* has a powerful (dominant on the spectrum) 12-year cycle of species abundance. This rhythm became stable, fitting to a similar cycle of precipitation (the rainiest years have a 12.6-year cycle there) and also to the 12-year cycle of Lake Chany level dynamics, the so-called Barabinsk natural cycle. Every 11–13 years, the increase in the lake level, as well as abundant precipitation, leads to the flooding of the shores of the lake and the formation of temporary reservoirs, eventually improving the conditions of larva existence. Apparently, such conditions—the maximum abundance of water bodies and a favorable water regime—are necessary for the successful development of *S. vulgatum* larvae. The remaining three species also depend on the hydrological characteristics of Lake Chany, fitting to them in other cycles.

We recorded the longest period of rhythm in this group of odonates for *S. vulgatum*: it is about 35 years. The length of our series does not make it possible to include even one such cycle, so it appears on the spectrum as a peak with a very wide base; its true value is between 30 and 45 years. The same cycle exists in the spectrum of the level (42.7 years) and the mirror (39.4 years) of Lake Chany. Doganovskii (2007, p. 109) noted that drainless Lake Bolshie Chany has 40–42-year level fluctuations. Apparently, this is one of the main cycles of the level changes for both lakes and the adjustment to it can be regarded as the most effective adaptation to local conditions.

There is a 18-year cycle of small power in the long-term dynamics of *S. danae*. In this area, it can fit to the close 16-year rhythm of the June temperatures (Table 4). June is the key month in the development of larval populations of the sympetrums: larvae of the older stages are molting larvae of final stage are ready to emerge from water reservoirs. Perhaps *S. danae* bets on June having stable and good water heating for replenishing its usual low population. And it happens every 16 years. Perhaps, for the same purposes, the species is synchronized with the powerful 18-year cycle of the level of Lake Chany.

A 24-year cycle dominates in power in the spectrum of long-term variation of *S. flaveolum* abundance. This is a cycle close to the Brickner cycle, well manifested in the entire vast area of Western Siberia. The phases of the moistening of the landscape change under its influence in Baraba and dry warm periods are replaced by cool and moist ones (Fefelov, 1999). It is very adaptive to adjust to this periodicity of climate change. The 28-year cyclic changes in April and May temperatures can also contribute to this adaptation.

CONCLUSIONS

Unified processing of data on the 31-year course of abundance dynamics of populations of four odonate species of the genus *Sympetrum* was used to construct spectra of harmonic components (cycles); their main parameters (period, phase, and power) were calculated. All spectra showed species specificity.

The interspecies differences in odonates of the genus *Sympetrum* are very poorly manifested at high frequencies due to a strong overlap in the values of parameters of the rhythms. In middle frequencies, the interspecies differences become larger. The largest power values have 5- to 6 and 7- to 8-year cycles. It is interesting that the changes in the structure of dominance in sympetrum odonato-complexes occur with the same frequency. At low frequencies the differences between species become even more pronounced: *S. danae* has an 18.6-year cycle of low power; in *S. flaveolum* it is 24.4-years, close to the Brickner one and dominant in power; *S. vulgatum* has 12-year and about 35-year cycles of high power. Only the *S. sanguineum* spectrum does not contain harmonics in the low-frequency zone; this species has only one long and powerful rhythm of abundance in the mid-frequency zone, 7.6-year, which in part can cause its small number.

The species of odonates of the genus *Sympetrum*, in addition to various cycles of population dynamics, also have similar cycles. This similarity is relative, since the cycles differ in the ratio of powers and/or phases. Thus, similar cycles with different phases may indicate specific interspecies interactions, leading to the separation of populations of sympatric species over time. As a result, medium and small species reach their maximum number at the minimum number of numerous species. Similar cycles with identical phases can indicate the ability of species to increase their numbers synchronously with any of the closely related species. Moreover, depending on the harmonic power, this synchronism can be expressed both in an increase in the number (for example, with the improvement of the forage base) or in its decrease (for example, with the growth of competitive tension).

Odonate species of the genus *Sympetrum* have the ability (adaptive) to adjust their powerful harmonics of the number fluctuations to the corresponding environmental and climatic factors. Therefore, their population rhythms will not fade. All sympetrum species can synchronize fluctuations in their numbers with 2–3 and 4- to 5-year fluctuations of the local climate. Each species also had its own specific synchronization with important environmental and climatic rhythms: *S. danae* is synchronized with the 18-year cycle of the level of Lake Chany and with 16-year cycle of June temperatures; *S. flaveolum* with the 24-year Brickner cycle, with the 8-year cycle of precipitation, and with the 28-year cycle of April and May temperatures; *S. vulgatum* with the 40- to 42-year cycle of the level of Lake Chany, with the 12-year cycle of precipitation, and with the 7-year cycle of April and June temperatures; and *S. sanguineum* with the 7.1-year cycle of April and June temperatures.

The following regularity could be assumed during a comparison of the spectra of sympatric species of the genera *Coenagrion* and *Sympetrum*: the more similarity of the species ecological standards is manifested (as for odonates of the genus *Sympetrum*), the more distinguishable their frequency spectra will be (by the number of cycles, the value of the periods, phases).

An analysis of the spectral characteristics of the long-term dynamics of the abundance of the studied species (both within the genus *Coenagrion* and within the genus *Sympetrum*), considering their ecological features, clearly demonstrated the adaptive nature of interannual population fluctuations: the species, through their rhythms, are adjusted to each other and their environments in accordance with evolutionarily acquired experience in coexisting. Perhaps this rhythmic adjustment helps the taxonomically and ecologically related species coexist in a single space and time.

ACKNOWLEDGMENTS

We sincerely thank A.B. Shcherbakova (Institute of Systematics and Ecology of Animals, Novosibirsk) for assistance in collecting field material; V.V. Glupov, director of the Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, for inspiring us in our research and providing a package of spectral analysis programs; and A.V. Tarnovskii, developer of the Harms software, for consultations on calculations. This study was supported by Russian Foundation for Basic Research (project no. 18-04-00725a), as well as by the Program of Fundamental Scientific Research (FSR) of the State Academies of Sciences for 2013–2020, project VI.51.1.7. (AAAA-A16-116121410123-1).

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Translated by T. Kuznetsova