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SHORT COMMUNICATIONS

Cyclicity in the Long-term Population Dynamics of Diving Ducks

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Waterfowl are one of the best-studied animal groups. Research on their breeding biology, behavior, migrations, and wintering has largely explained their population dynamics and factors on which they depend. In most cases, conclusions based on long-term observations on these birds concern certain trends in their abundance, but there is also evidence for the existence of waterfowl population cycles with different periods [1–3]. Using the discrete Fourier transform and autocorrelation function analysis, Söderholm [4] has shown that the population abundance of the common pochard (one of the species we study) on its breeding grounds in Sweden and Latvia fluctuates with a period of about 5 years.

Cyclic changes in animal population density have been studied for a long time [5]. It has been shown, in particular, that population dynamics are multiperiodic [6], which interferes with visual perception of periodicity in graphic plots. Therefore, cyclicity is increasingly analyzed using spectral representation of the corresponding process, which makes it possible to reveal the entire set of periodic components of the dynamics and compare their powers [7].

Here, we consider population fluctuations in two diving duck species, the common pochard (*Aythya ferina*) and tufted duck (*A. fuligula*). The purpose of this study was to estimate the parameters of cycles in the dynamics of their abundance in different geographic populations, compare these parameters, and reveal natural oscillations providing for the stability of population cycles.

Long-term studies (1969–2011) on the ecology of ducks during the breeding season were performed on Lake Krotovo in the Karasuk district, Novosibirsk oblast (53°72′ N, 78°02′ E). The surface area of the lake varies between 345 and 485 ha, depending on water level. Censuses of duck nests were taken every year, at approximately 10-day intervals, by making a complete survey of islands and the margin of floating mat on permanent plots located all over the lake perimeter. A total of 1843 *A. ferina* and 2228 *A. fuligula* nests were found, and variation in the number of nests between years was evaluated.

For comparative analysis, we used long-term series of data on censuses of duck nests over different periods of time. Latvian ornithologists performed relevant studies on Lake Engure (57°15′ N, 23°07′ N), where *A. ferina* ranked first among ducks in the number of nests, and described the population dynamics of this species over the period from 1972 to 1992 [8]. The data on *A. fuligula* included a 22-year series of summer censuses (1958–1979) on Lake Engure [9] and 31-year series of censuses (1977–2007) taken on islands in the Maloe More Strait, Lake Baikal (53°09′ N, 106°85′ E) [10].

Data on the North Atlantic Oscillation (NAO), which dictates much of the climate variability from the eastern seaboard of the United States to Siberia [11], were from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based. The table of seasonal NAO indices was used to selected for analysis time series of the winter index (December–February, NAO-DJF) and spring index (March–May, NAO-MAM) for the period of 1969 to 2011.

Spectral analysis is a popular technique for revealing and describing periodic oscillations in physics and biology. We used the program for spectral analysis owned by the Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences. Power spectral density (PSD) was estimated by Welch's method [12]. All calculations were made using the free software package GNU Octave (http://www.gnu.org/software/octave/; https://ru.wikipedia.org/wiki/GNU_Octave) featuring a high-level programming language and an interactive interface for solving linear and nonlinear mathematical problems. In particular, Welch's method was implemented using the pwelch function in Octave-Forge (http://octave.sourceforge.net/signal/function/pwelch.html). Each analysis of a long-term data series on the number of nests generated a PSD distribution by periods, which was then expressed as a percentage of the maximum value. Peaks on the

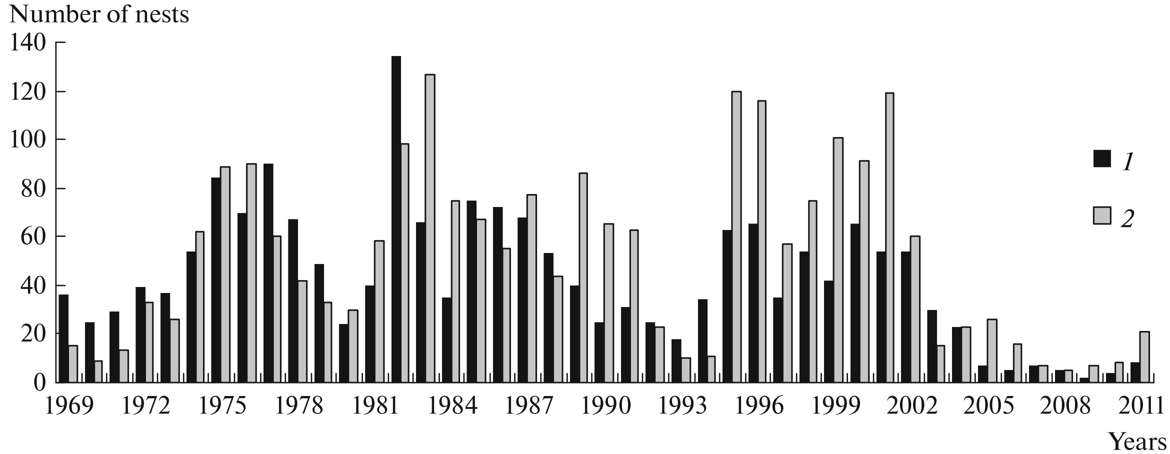

Fig. 1. Chronogram of changes in the numbers of (1) *Aythya ferina* and (2) *A. fuligula* nests on Lake Krotovo (1969–2011).

resulting power spectrum corresponded to basic periodicities.

Figure 1 shows data on the abundance dynamics of diving ducks nesting on Lake Krotovo. The amplitude of changes in abundance between years is fairly high in both species: the numbers of nests may differ by an order of magnitude, changing gradually or rising and dropping abruptly. It can be seen that the directions of these changes in *A. ferina* and *A. fuligula* coincided in certain years but were opposite in other years.

Using this chronogram, it was difficult to reveal the cycles characteristic of the abundance dynamics of each species, and the time course of changes in the numbers of nests was expressed on a frequency scale (Figs. 2b, 2d). Thus, new information on the cyclicity of changes in abundance was obtained at the expense of information on their magnitude. To improve representativity of general conclusions, we analyzed long-term data series on the numbers of nests of both species on Lake Engure (Figs. 2a, 2c) and of *A. fuligula* on Lake Baikal (Fig. 2e). Published data on nest censuses over less than 20 years were not used.

Curves of the rhythms of abundance fluctuations during the nesting season plotted on the frequency scale are a superposition of several distinct periodic components (Fig. 2.). The dynamics of *A. ferina* nest numbers on Lake Krotovo and Lake Engure have three common rhythms with cycles of about 4.5, 3, and 2.5 years, with the first rhythm being dominant in power. Dominant low-frequency rhythms have periods of 25 years on Lake Krotovo and 17 years on Lake Engure. The difference can be explained by the fact that the series of available data on Lake Engure is shorter. Two more components with 6- and 11-year periods are distinct in the spectrum for Lake Krotovo but absent in the spectrum for Lake Engure.

The dynamics of *A. fuligula* nest numbers on Lake Krotovo have a dominant 7-year rhythm that is absent from the spectra of this species in other regions. Other rhythms have almost the same periods in all regions but differ in power. All spectra include (1) a low-frequency cycle with a period of 14–17 years; (2) a distinct approximately 4-year cycle, which is dominant in the spectrum for Lake Engure, subdominant in the spectrum for Lake Baikal, and third in power in the spectrum for Lake Krotovo; and (3) a high-frequency cycle with a period of 2–2.5 years that is dominant in the spectrum for Lake Baikal, third in power in the spectrum for Lake Engure, and fourth in power in the spectrum for Lake Krotovo.

Interspecific comparisons show that the main periodic components of the abundance spectra of *A. ferina* and *A. fuligula* on Lake Engure are in close frequency bands. The cycle dominant in power has a period of about 5 years in *A. ferina* and 4 years in *A. fuligula;* the 3-year component is characteristic only of *A. ferina*. Differences in the dynamics of abundance between these species are more numerous in the spectra for Lake Krotovo.

In the northern Kulunda lowland, both these species are common, sometimes highly abundant, and populate the same habitats but differ in ecological preferences. For example, males and females in *A. ferina* overwinter in different areas [13] and form pairs in nesting grounds where lek mating takes place, with males being much more abundant than females. In *A. filigula,* pairs are usually formed in wintering areas or during migrations. It is only in some years that groups of ducks display lekking behavior after arrival to their nesting lake. The diet of both species includes plant and animal foods, but *A. ferina* is mainly herbivorous and can make up for shortage in any kind of food, whereas *A. fuligula* prefers animal food. This may explain differences in the timing of breeding, which starts 1012 days earlier in *A. ferina* than in *A. fuligula*. Specific biological features considered above may account for differences in the response of duck populations to the pattern of spring events and