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Disclosure of Biotopical Groups in the Population of the Dragonfly *Coenagrion armatum* (Charpentier, 1840)

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Abstract—The spatial-temporal distributions of the dragonfly *Coenagrion armatum* in Lake Fadikha with edging overgrowth in the Barabinsk forest steppe are described. It is discovered that the local population of this species is divided into two biotopical groups. The specimens of one group develop in the water area and do not migrate to the shore after metamorphosis; in the other, dragonflies develop in the reeds and migrate to the shore for additional feeding after metamorphosis.

Keywords: dragonflies, *Coenagrion armatum*, density, imago (larva) hemipopulation, stretch of lake, reed edge, intrapopulation topical groups

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INTRODUCTION

Produced from water larvae, young imagines of dragonflies fly from the water area as amphibiotic insects to the shore, where they feed, spend nights, and find shelter in bad weather. On some days imagines become pubescent and return to the water bodies for reproduction. Sometimes this simple scheme is complicated by imago migration between the water areas and even a long delay of preproductive development (Corbet, 1999; Kharitonov, and Popova, 2011).

Studying the populations of dragonflies in Lake Fadikha in the Barabinsk in southwestern Siberia, we faced an unknown variant of spatial distribution of imagines after they emerge from larvae. Two intrapopulation tropical groups were discovered in the species *Coenagrion armatum* (Charpentier, 1840) in the local population of one of the lakes with a strong reed edge. Larvae of one group grow in the littoral reed bed, and after emerging imagines fly to the shore according to the common scheme; larvae of other group live among submerged vegetation on the open stretch of lake that is cut off from the shore with a reed edge and the imagines do not leave the lake stretch after having become winged, but they additionally feed on and reproduce in the same place. An assumption about the possibility of such unusual philopatry of dragonflies expressed in the attachment to one stretch of lake arose on the basis of a visual observation of imago behavior and a series of records of imagines and larvae (Popova, 2006; Kharitonov, and Popova, 2011). The aim of the given research was to obtain reliable quantitative proofs of existence of such groups. With this purpose, the terms of emergence, seasonal dynamics of abundance, space distribution, and migration of imago *Coenagrion armatum* were studied in Lake Fadikha from May to July of 2012.

† Deceased.

MATERIALS AND METHODS

The object of study. The dragonfly *Coenagrion armatum* is widespread in the forest and forest-steppe zones of Eurasia, but it is most numerous in southwestern Siberia, particularly in the district where the studying was held (Popova and Kharitonov, 2012). This species is most recognizable in the genus *Coenagrion* by a complex of morphological features and is easily identified at a distance of 1–2 m, simplifying work with the dragonflies in the field. The life cycle is univoltine. Imagines are emerged from larvae in spring earlier than other species of dragonflies: usually in the middle of May in studied place. The maximal number of imagines is from the end of May to the beginning of June, and last specimens are registered until the end of the first decade of July. The eggs are laid from the end of spring to the beginning of summer, and by the end of autumn the most of larvae finish their development and hibernate in their final age.

The place of studying. The studying was held in the period from May to June of 2012 in the central part of Barabinsk forest steppe on the territory of Novosibirsk Province (southwestern Siberia). The data on biotopical peculiarities of population *C. armatum* were obtained in the northern part of Lake Fadikha (54°36′ N, 78°12′ E) that is located 5 km eastward of Lake Small

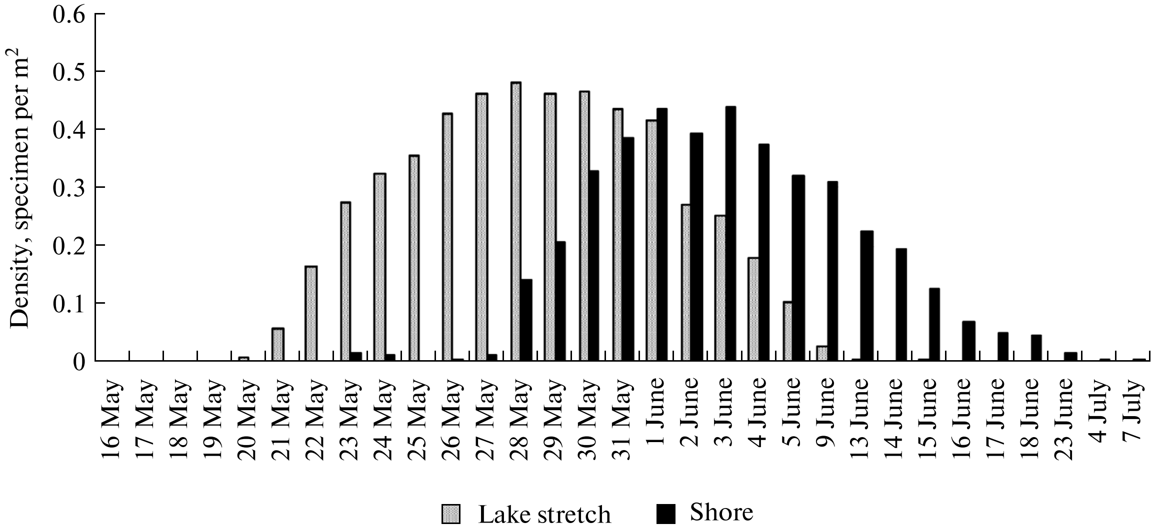

Fig. 1. Dynamics of density of imago hemipopulation *Coenagrion armatum* on the lake stretch and on the shore of Lake Fadikha in 2012.

Chany in falling between elongated hills (below manes) on the forest-steppe landscape. The lake is flowing, shallow, and reed-edged (*Phragmites australis*) with an area of 5 km^2. Bladderwort (*Utricularia vulgaris*), duckweed (*Lemna trisulca*), and a small amount of hornwort (*Ceratophyllum demersum*) grow in small glades of a strong reed thicket. In the studied part of the lake, the reed edge (relative littoral) stretches from the shore line into the depth of the lake for about 80 m (the average depth is 0.4 m); this is followed by a 1-km-long lake stretch (relative sublittoral) with an average width of 120 m (average depth is 0.7 m). Behind the lake stretch the open waters begin (average depth is about 1.5 m), free from all types of water microphytes (profundal). The stretch of lake is an interchange of an open water area with areas covered with thinned reed. The stretch of lake is isolated from the profundal with a stripe of thick tall reedbeds. About one-eighth of the stretch is covered with reed and the whole area of water is overgrown with lavish submerged vegetation, among which bladderwort and hornwort prevail. Data on qualitative and quantitative composition of hydrobionts on the stretch and littoral reeds have been published earlier (Popova and Smirnova, 2010).

Attached to the studied sector of Lake Fadikha, the landscape is open sloping upland (500 m wide) stretched between the lake and the mouth of the Kargat River. The top and slopes of the mane are occupied with herb–bunchgrass steppefied meadow and its littoral area attached to the lake is covered with reedgrass and licorice-reedgrass meadows that are further considered a unified littoral meadow: land and ground or littoral biotope. It is known that many species of dragonflies which do not belong to the number of those prone to far migrations mainly accumulate in littoral biotopes after emergence no more than 250 m from the lake (Bried, Ervin, 2006), so records on the land were conducted at the same distance from the water.

Description of Methods and Calculations

Quantitative data on the hemipopultion of larvae (i.e., on the larva part of species population) were obtained by two methods: (1) regularly passing the hydrobiological net over submerged vegetation 1 m in length; (2) a water biocenometer—metal cylinder with a square section (25 × 25 cm) taking 1/16 m^2 of the lake being studied (Nikolaeva and Ol'shvang, 1978).

Autecological parameters of *C. armatum* were studied: terms of imago emergence, seasonal dynamics of number, and spatial distribution and migration of imagines. Emerging was estimated using a buoyed trap, the seasonal dynamics of imago number was estimated recording dragonflies on band transects, and the spatial distribution and migration of imagines was estimated by marking dragonflies (the capture-mark-recapture method). If, when studying the stretch group it is possible to achieve all given methods directly on the lake stretch and accordingly to trace all set-up parameters, to study the reed group directly in the reeds it is possible to apply the method of buoyed traps only because neither recording them on the transects nor marking in the impenetrable reeds are possible. Under the hypothesis that all dragonflies from the reed edge after emergence migrate to the shore, composing a single reed and shore group, the assessment of their migration and dynamics of number may be carried out on the littoral meadow. Therefore other than the two main water biotopes (lake stretch and reeds), a third one was taken: the land one (littoral meadow). Each of three mentioned methods, on the

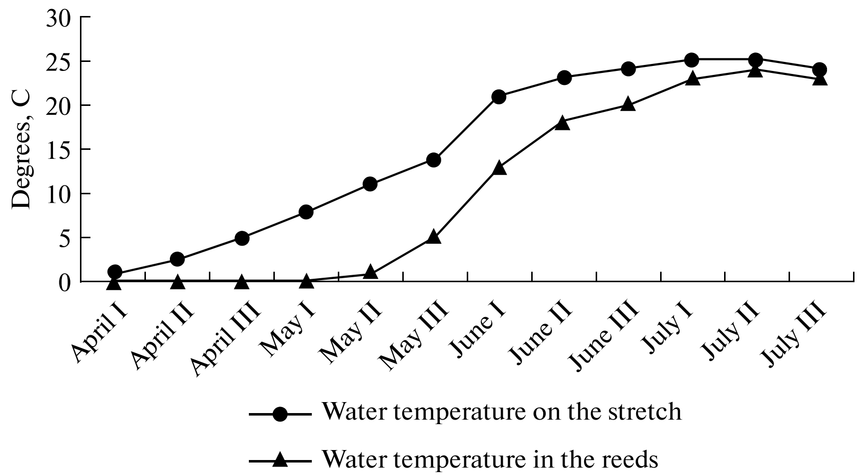

Fig. 2. Average decade temperatures of water on Lake Fadikha in 2012.

one hand, is oriented towards studying a specific phenomenon in the life of population, and on the other hand, it makes it possible to calculate the absolute number that is "the nongraded number of specimens of species or their group within a certain space" (Reimers, 1990, P. 575). The absolute number may be transferred into the density of population. Marking method is one of the most reliable methods of assessing the absolute number of population (Caughley, 1977; Begon, 1979). In order to ensure the possibility of comparing studied biotopical groups, it is necessary to calculate the total seasonal values of the number and density of *C. armatum* directly reached by the method of buoyed traps and mediately by marking and recording on the transects. The latter two methods are acceptable only when the duration of mass flying of species is not long (no more than 2 weeks, as in *C. armatum*), whereas corresponding to this time (maximal) number agrees with the total number of species for the season. Each of applied methods has its advantages and disadvantages and cannot be regarded as priority one for number calculations. In total, all three methods complement each other and increase the accuracy of final result; therefore, apparently, an arithmetic mean of results of all three methods reflects the situation more accurately when it is possible (on the lake stretch).

The area of lake stretch (area of water) is 120 × 1000 m, which makes 120000 m^2 (including the water area covered with thinned reed, 15000 m^2); the reed edge is 80 × 1000 m = 80000 m^2; and the littoral meadow is 250 × 1000 m = 250000 m^2.

Recording dragonfly imagines on the band transects: water and land. The band transect is a stripe of visual recording with set-up length and width. Altogether, from May 16 to July 7 on the lake stretch and on the shore, there were 31 recordings in each biotope, the total length of which was 12.4 km on the stretch and 6.2 km on the shore. For every recording, the density of hemipopulation of imagines was calculated (i.e., the imago part of species population), which is why the number of observed specimens was divided in the transect area; the diagram of seasonal dynamics of species number on the stretch and in the reeds was constructed according to the density index (Fig. 1).

The 400-m-long and 2-m-wide (i.e., area of 800 m^2) water transect was recorded on a boat and divided into half for a better embracement of the biotope: the first (200 m) was running on the stretch edge nearby the reed edge and the second (200 m)—in reverse direction—was in the central part of the stretch. From 31 recordings carried out on the transect, the maximal number in 384 specimens per on one recording was marked on May 28 (Fig. 1). The transect area was 1/150 part of the water area of stretch; correspondingly, the maximal seasonal num-

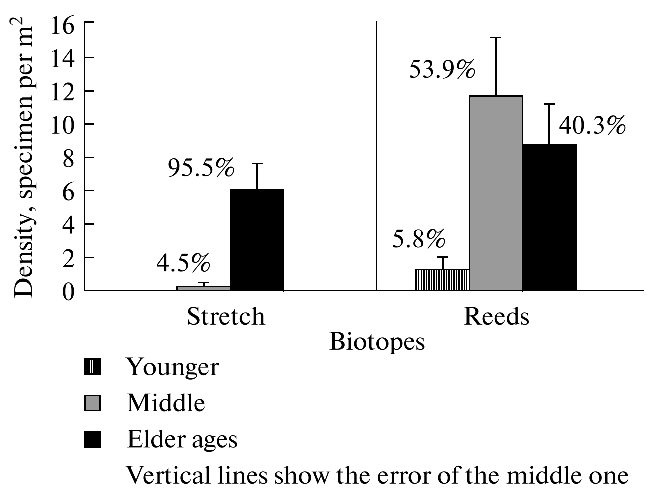

Fig. 3. Age structure of hemipopulation of larvae *Coenagrion armatum* in biotopical groups on Lake Fadikha in the first decade of May 2012.

ber of *C.armatum* on the whole stretch is equal to 384 specimens multiplied by 150, which makes for 57600 specimens, and the maximal seasonal density of imago hemipopulation on the stretch is equal to 384 specimens divided by 800 m^2, which makes 0.48 specimens per m^2.

The land transect was twice as short and narrow (200×1 m = 200 m^2), because it is more difficult to observe small dragonflies in the grass than on the water. On the same grounds, it is divided into two halves: the first one (100 m) was running along the lake shore in the licorice-reedgrass meadow; the second one (100 m)—in the reverse direction—was 40 m from the shore in the herb–bunchgrass steppe meadow. From 31 recordings carried out on the transect, the maximal number in 88 specimens was marked in June 3 (Fig. 1). The area of the transect was 1/1250 part of the whole area of land biotope and, accordingly, the maximal seasonal number of *C. armatum* on the whole littoral meadow is equal to 88 specimens multiplied by 1250, being 110 000 specimens; the maximal seasonal density of the imago hemipopulation on the littoral meadow is equal to 88 specimens divided by 200 m^2, being 0.44 specimens per m^2.

Recording dragonfly imagines using the capture-mark-recapture method. The marking of dragonflies with different labels made it possible to trace whether dragonflies of the stretch group fly to the shore and reed ones fly to the stretch or they are attached to their biotope.

Accordingly, the marking was held in two biotopes: on the lake stretch and in the meadow. The marking in each of biotopes was performed in the days of a maximal number of imagines in the biotope. Labels were put with bright red water-resistant lipstick and were easily seen during the whole period of observation. The calculation of the number was done according to the formula $N = M(n + 1)/m + 1$, where M means the number of specimens that were caught and marked and then released, n means number of repeatedly caught specimens, and m is number of marked specimens amongst repeatedly caught ones.

From May 24 to 27, on the lake stretch, dragonflies were marked on the 200-m-long and 60-m-wide water area (12000 m^2). The dragonflies for marking were caught over the water from a light maneuverable two-seater boat pushed with a punt pole. The basal part of wings—the part between the wing root and the nodule in the area of the wing quadrangle—was marked. In total, 350 imago specimens (182 males and 168 females) were marked. On May 28, in the case of the maximal number of *C. armatum*, repeated catching was performed on the lake stretch: 330 specimens, among which 21 were marked. The calculation according to the abovementioned formula showed that, on the stretch with an area of 12000 m^2 where the marking was carried out, the number of dragonflies $N = 350(330 + 1)/21 + 1 = 5266$ specimens. This result can be considered reliable, because its correspondence to the estimated error (SE_N=1061) is equal to 5.0, which complies with the method terms (Caughley, 1977). The stretch area where the marking was done is one-tenth of the whole water area and, consequently, the maximal seasonal number of *C. armatum* on the whole investigated stretch area comprises 5266 specimens multiplied by 10, being 52660 specimens; the maximal seasonal density of the imago hemipopulation on the stretch is 5266 divided by 12000 m^2, being 0.44 specimens per m^2.

On the littoral meadow, the dragonflies were marked on an area 200 m long and 100 m wide (20000 m^2) on May 30 and 31. The distal wing part, being rather more proximal from the pterostigma, was marked. In total, 500 specimens (237 males and 263 females) of imagines were marked. On June 1, in the case of the maximal number of *C. armatum*, the repeated catching of dragonflies was performed: 400 specimens were caught, among which 23 were marked. The estimation proved that, on a meadow with the area of 20000 m^2, where the marking was carried out, the number of dragonflies $N = 500(400 + 1)/23 + 1$, equaling 8354 specimens. This result also can be considered reliable, because its correspondence to the estimated error ($SE_N = 1620$) is equal to 5.2. The shore section, where the marking was carried out, is 1/12.5 of the studied littoral area; therefore, the maximal seasonal number of *C. armatum* on the territory is equal to 8354 specimens multiplied by 12.5, being 104425 specimens, and the maximal seasonal density of imago hemi population in the littoral meadow equals 104425 specimens divided by 250000 m^2, making 0.42 specimens per m^2.

Recording dragonfly imagines using buoyed traps. This method makes it possible to estimate directly the general seasonal numbers and density of *C. armatum*. With this purpose, on the stretch and in the depth of the reed edge, six traps of an original construction were installed: a trapeziform tent 2.5 m high from close-meshed netting fixed in the wooden frame 2×2 m and stated on the water surface by means of pegs. Each trap isolated the water section with reed, covering an area of 4 m^2, being a substrate for larva metamorphosis. At the highest part of the netting construction, there was a hole 10 cm in diameter where a wide plastic ring was sewed in. On the ring with the help of rubber, a thin transparent polyethylene disk was applied with VLN-11 entomological glue. Amphibious insects emerging inside the trap, including dragonflies, owing to the positive phototaxis and trapeziform construction, moved to its highest and brightest part and affixed to the removable disk, which was replaced with a new one every day. Three traps on the lake stretch and three on the reed edge made it possible to estimate the emerging with 12 m^2 in each of those biotopes and extrapolate the data on the whole territory.

During the season, 15, 19, and 21 emerged imagines entered each of three traps fixed into the reed stretch bed. The total seasonal density of dragonflies emerged on the area occupied with three traps comprises (15 + 19 + 21) specimens divided by 12 m^2, which is 4.6 specimens per m^2. The value of density cannot be extrapolated on the whole water area of the lake stretch for the following reason: though dragonfly larvae are distributed on the whole stretch rather evenly, before emergence they accumulate on the thin reed spread over the stretch as they crawl on the stems of reed for metamorphosis. Because this area of thinned reed occupies one-eighth of the whole water area, correspondingly the value of larva density is eight times bigger than the density on the stretch on the whole. Therefore, the total seasonal density of imago hemipopulation on the stretch equals 4.6 specimens per m^2 divided by 8, which makes 0.58 specimens per m^2, and the general number of dragonflies (total number) of studied species from the stretch biotope comprises 0.58 specimens/m^2 multiplied by 120000 m^2 and equals to 69600 specimens per season.

During the season, 6, 7, and 9 emerged *C. armatum* imagines entered all three traps fixed in the depth of the reed edge. The total seasonal density of dragonflies, emerged within the area occupied with three traps, was (6 + 7 + 9) specimens divided by 12 m^2, which is 1.8 specimens per m^2. The obtained value of density can be extrapolated on the whole area of the studied reeds and, correspondingly, the total number of dragonflies of studied species from the reed edge was 1.8 specimens/m^2 multiplied by 80000 m^2, which equals 144000 specimens per season.

Coordinates and all necessary distances on the territory and water area were measured using a Garmin eTrex Legend GPS navigator.

The water temperature on the stretch and on the reed edge was measured using a water thermometer fixed with movable clip on a centimeter-graduated rack. The readings were taken at 8:00 to 9:00 a.m. in the morning at three levels: at the bottom, at the middle water layer, and near the surface. On the lake stretch, the measurements were taken in its central part; on the reed edge they were taken at a distance of about 40 m from the shore.

RESULTS AND DISCUSSIONS

Biotopical differences in abiotic habitat conditions. Conditions of habitation existing on the open lake stretch and on the reed edge of Lake Fadikha are completely different, including such important parameter as the seasonal dynamics of the water temperature. During the ice-free season, the temperature of water on the stretch is on average 5°C higher than on the reed edge (Fig. 2). These differences become strongly apparent in spring. In May on the stretch in the average depth (30–35 m), the medium-decade water temperature is 9.5°C higher than in the reeds. In June and July these differences are 5.6 and 1.4°C, correspondingly. The ice on the stretch melts usually mid-April; afterwards, the water starts warming up quickly. In winter, the more shallow section of the reed edge freezes through the bottom and dense reed retains a thick snow mantle (up to 80 cm) for a long time; the near-bottom water sheet stays deep-frozen up to the end of May. The differences in hydrological and temperature regimes cause phenological differences between the stretch and the reed parts of the population of *C. armatum*.

Biotopical differences of age structure of larva hemipopulation according to average longstanding data of hydrobiological samples. In the first decade of May, the age composition of larvae of *C. armatum* on the stretch is rather homogeneous, because senior larvae make up 95.5%, middle ones make up only 4.5%, and junior larvae are completely absent (Fig. 3). This testifies to the fact that the higher temperature of the water on the stretch makes it possible for the majority of larvae to finish their life cycle during the vegetation season or hibernation, being ready for friendly synchronized imago emergence in spring. In this period the age composition of larvae in the reeds is completely different: the senior larvae make up 40.3%, middle ones 53.9% and junior larvae 5.8% (Fig. 3). Lower of the water temperature; unsynchronized imago emergence; and, correspondingly, extended period of eggs-laying result in the age composition of larvae in the reeds being heterogeneous in spring.

Biotopical differences of number and density of imago hemipopulation. *The stretch topical group.* The method of recordng on the transect showed that, on the lake stretch, the first *C. armatum* imago appeared on May 20; during the following 6 days their number rapidly increased and for the week it remains relatively fixed. From the first days of June it started sharply decreasing, the last single specimens were observed in the middle of June (Fig. 1). The maximal seasonal number and density were observed generally on May 28: the method transect is 57600 specimens and 0.48 specimens per m^2; the marking method is 52660 specimens and 0.44 specimens per m^2 correspondingly. Using the method of buoyed traps, the general seasonal reproduction of dragonflies of studied species from the stretch biotope—69600 specimens—and the total seasonal density of imago hemipopulation on the stretch—0.58 specimens per m^2—were estimated. Obtaind by means of different methods, these values were rather similar because the general life time of imago of *C. armatum* on the stretch is rather short (about 3 weeks) and moreover all emerged dragonflies are accumulated within the lake stretch. Therefore, the arithmetical mean of results of all methods should reflect the situation more accurately; it is equal to total seasonal number 59953 ± 6240 specimens and a density of imago hemipopulation of 0.5 ± 0.05 specimens per m^2. Below, while comparing the sizes of two biotopical groups, for the stretch group we will use these avaraged numbers in particular.

After marking (on May 24–27), the dragonflies with the stretch label were observed every day on the water area at boat recordings up to June 5; while no specimen with the same label was observed on the land in littoral biotopes because the specimens of the stretch group did not migrate to the shore.

Reed topical group. Despite the fact that, on the lake stretch, about 60000 *C. armatum* imagines were estimated by the end of the third decade of May, in the littoral biotope in the case of daily recording on the transect, no dragonfly of this species was observed until May 23, and starting from 23 to 28 May they were found rarely here and were obviously the first representatives of the other group: the reed part of population (Fig. 1).

On the reed edge, the intensive emergence of imagines started on May 28, when the first juvenile imagines appeared on the shore in considerable numbers; simultaneously, they were found in traps in the depth of the reeds. From that day they were registered on the littoral meadow every day. Until the first days of June their number increased and afterwards it started decreasing gradually. The last single specimens in the littoral biotopes were observed at the end of the first decade of July.

After the marking (on May 30–31), the dragonflies with a reed label were observed at transect land recordings every day until June 14, while no specimen with the same label was found on the lake stretch because representatives of the reed group did not migrate to the stretch.

The maximal seasonal values of number and density in the littoral biotope was marked on the first days of June: the method of transect showed 110000 specimens and 0.44 specimens per m^2; the method of marking showed 104425 specimens and 0.42 specimens per m^2, correspondingly. Like results from the stretch using different methods, the values were rather similar. Using the method of buoyed traps, the general seasonal reproduction of dragonflies from the reed edge—144000 specimens—and total seasonal density of imago hemipopulation in the reeds—1.8 specimens per m^2—were estimated. The differences between maximal values obtained by the method of buoyed traps were bigger in the reeds than on the lake stretch. This difference is quite explainable. The density is 4.2 times higher (1.8 specimens per m^2) on the reed edge than on the meadow (on average 0.43 specimens per m^2) as the dragonflies migrating to the littoral meadow ($S = 250000$ m^2) are distributed on the whole territory, the area of which is bigger than the area of the reed edge ($S = 80000$ m^2), and their density is accordingly decreasing. The much greater general number in the reeds (144000 specimen) in comparison with the meadow (on average 107213 specimens) can be explained by the fact that the different ages of larvae in this biotope causes the extended emergence of imagines; and the method of buoyed traps is the only way to reflect the real scale of emergence of the dragonflies from larvae. Therefore, comparing the sizes of two biotopical groups, we will use the data obtained by buoyed traps for the reed group.

The total seasonal number of *C. armatum* on the reed edge (144000 specimens) was 2.4 times greater than on the stretch (59 953 specimens).

The total seasonal density of imago hemipopulation of *C. armatum* on the reed edge (1.8 specimens per m^2) was 3.6 times higher than on the lake stretch (0.5 specimens per m^2). According to longstanding data, such a correlation for this water body was estimated for the population of larvae of Zygoptera on the whole (Popova and Smirnova, 2010).

CONCLUSIONS

The data on how local populations of *C. armatum* on the lakes with reed edges may be differentiated into biotopical groups was obtained and published earlier (Popova, 2006; Kharitonov and Popova, 2011). However, before marking it was not certain whether the life cycle of dragonflies on the lakes isolated from the shore by the vast reeds is really gone within the limits of these water areas without migrations to land biotopes. The result of marking of 850 specimens of *C. armatum* on Lake Fadikha in spring confirmed the fact of philopatry of the stretch part of the dragonfly population. None of the 350 specimens marked on the lake stretch was found on the shore, and all dragonflies with stretch labels were registered only within the limits of the water where they had been marked up to the end of flying of imagines. Also, none of the 500 specimens marked on the shore was found on the lake stretch and all dragonflies with shore labels were regularly found on the littoral meadows or on the reed edge where they were reproducing.

An estimation of the total seasonal number of the stretch and littoral biotopical groups also confirmed their autonomy because, within the limits of every biotope, the values of number and dynamics stayed unchanging. The appearance of imagines on the stretch happened a week earlier than intensive emergence started in the reeds, the number reached maximal values quickly and decreased rapidly on the first days of June, and in the middle of the month the dragonflies disappeared entirely on the stretch. The number of imagines in the reeds increased slowly and stayed high longer, and the last dragonflies from the reed group disappeared at the end of the first decade of July.

On the whole, all stages of the life cycle of the stretch group are considerably more synchronized, and the imago stage is noticeably shortened in comparison with the reed group. Imagines on the lake stretch appear in the second decade of May, when the vegetation cover in the land biotopes is insufficiently formed and poor in small insects that are food for the dragonflies. However, at this time water area with thinned reeds on the stretch, there are numerous spring species of chironomids, being a nutritive base for the dragonflies. The thick reeds surrounding the stretch creates an uneven wall of vegetation with many shelters from wind and rain, which is especially important in May as it is the month with the windiest and most unstable weather in the Barabinks forest-steppe. Moreover, according to our observations *C. armatum* is faced with minimal competition for the egg-laying places from other species in the short period of their maximal number in stretch; but at the end of May, the more numerous *Coenagrion lunulatum* (Charpentier, 1840) forces them out to the stretch periphery. All these circumstances make the habitation of dragonflies in the lake stretch more comfortable in the second part of May than in the shore biotopes and maintain the stability of the existence of the stretch biotopical group.

Imagines of the reed group emerge later and are more numerous in the end of June (when the vegetation cover is completely formed in the littoral biotopes) and rather tall grasses provide shelter on the shore of bad weather and a nutritive base, the latter is not only as amphibious chironomids and mosquitoes, but other small land insects. Therefore, the life cycle of the dragonflies of the reed group passes according to a scheme typical for these predators: just after emerging they migrate to the shore for additional feeding, and, from the beginning of reproduction, the rotation between reproductive and trophical stations is established, i.e., reed and shore.

Despite the known regularities of existence of dragonfly populations, the adaptive plasticity of these insects is so high that they can find and achieve nonstandard ways of their development, thereby enhancing the efficiency of ecosystem functioning in general. Dragonflies as amphibious organisms are an important link in the process of formation of substance and energy streams not only inside the ecosystems but also between them. For the efficiency of these streams it is necessary for the population to use space trophical and other environment resources to the maximum, and this can be promoted by its division into biotopical groups. Biotopical groups extend the space and time limits of the existence of the local population, increase the capacity of its life environment for the species, and ensure its well being in rather severe and unstable conditions in Siberia.

The division into biotopical intrapopulation groups on particular lakes is probably not a unique phenomenon for the species of *C. armatum*. According to all indications, this phenomenon is typical, at least, for another more spring species, *C. lunulatum*, but it is necessary to conduct additional tests to confirm this.

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