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Mosquito Distribution in Northwestern Russia: Species of the Genera *Anopheles* Meigen, *Coquillettidia* Dyar, *Culex* L., and *Culiseta* Felt (Diptera, Culicidae)

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Abstract—Records of 16 species of the mosquito genera *Anopheles*, *Coquillettidia*, *Culex*, and *Culiseta* (Diptera: Culicidae) in Northwestern Russia are mapped. The values of the sum of active temperatures above 0°C were shown to correlate with the position of the northern range boundaries of mosquito species, according to which 16 species were included in 4 distribution groups.

Keywords: mosquitoes, distribution, Northwestern Russia, sum of active temperatures above 0°C, Diptera, Culicidae, *Anopheles*, *Coquillettidia*, *Culex*, *Culiseta*

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Mosquitoes (Diptera: Culicidae) are widespread over the whole Northwestern Region of Russia[1] (NWR, Fig. 1). Females of some mosquito species bite humans and are responsible for the transmission of medically important pathogens and parasites such as viruses, bacteria, protozoans, and nematodes. For example, Sindbis, Batai, and California encephalitis viruses are known to be transmitted in NWR by mosquitoes of the genera *Aedes*[2] Meigen, 1818, *Anopheles* Meigen, 1818, and *Culex* Linnaeus, 1758 (Lvov et al., 1989; Alkhovsky, 2016). A study of the associations between mosquitoes and specific pathogens requires both correct identification of the vector species and reliable data on the mosquito fauna in the study region.

In this article we continue the study of bloodsucking insects in NWR, which has been carried out at the Zoological Institute of the Russian Academy of Sciences (ZIN) since 2005. First, we made a general outline of the regional faunas of mosquitoes, blackflies (Simuliidae), horseflies (Tabanidae), and biting midges (Ceratopogonidae) (Medvedev et al., 2007); then mosquito distribution was considered in greater detail (Aibulatov and Khalin, 2019; Aibulatov et al., 2020; Khalin and Aibulatov, 2020, 2021).

During further analysis of the northern range boundaries we have mapped the records of 16 mosquito species of the genera *Anopheles*, *Coquillettidia* Dyar, 1905, *Culex*, and *Culiseta* Felt, 1904 in the whole territory of NWR. In this article we examine all the species of Culicidae present in the NWR fauna, with the exception of *Aedes* species. We use our earlier data (Khalin and Aibulatov, 2020), e.g., the results of identification of the material collected by S.V. Aibulatov and A.V. Khalin

[1] The Northwestern Region of Russia in our interpretation corresponds to the Northwestern Federal District of Russia, which includes Murmansk (MP), Arkhangelsk (AP), Leningrad (LP), Vologda (VP), Kaliningrad (KP), Pskov (PP), Novgorod provinces (NP), and the republics of Karelia (RK) and Komi. The Nenets Autonomous Okrug (NAO) is considered here separately from the rest of Arkhangelsk Province.

[2] We use the classification by Wilkerson and co-authors (Wilkerson et al., 2015), according to which the genus *Aedes* includes the subgenus *Ochlerotatus* Lynch Arribalzaga, 1891.

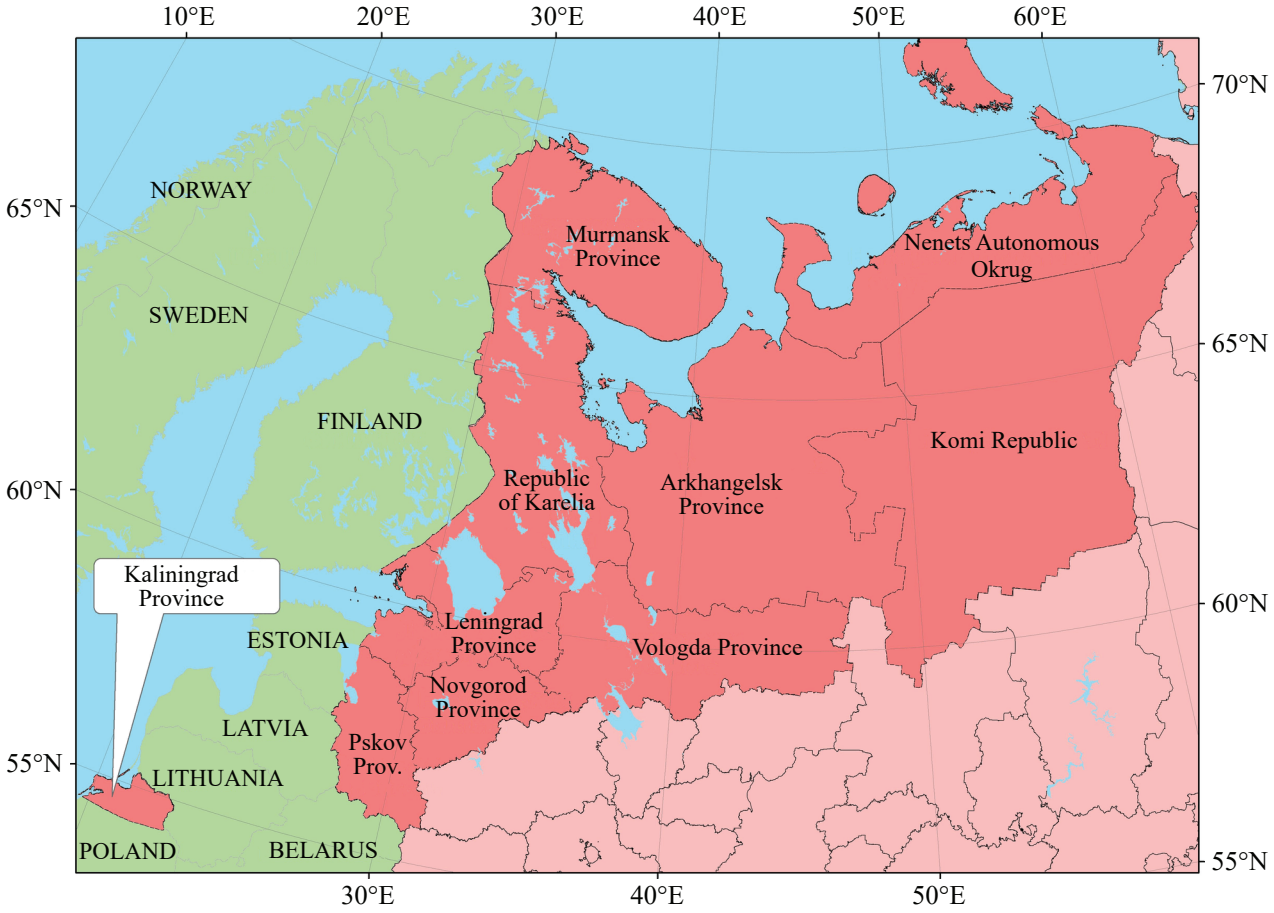

Fig. 1. The Northwestern Region of Russia.

and revision of the ZIN collection. In addition, it includes analysis of additional literature for some regions of NWR.

The distribution within NWR has been described for the following species: *Anopheles atroparvus* van Thiel, 1927, *A. beklemishevi* Stegnii et Kabanova, 1976, *A. claviger* (Meigen, 1804), *A. maculipennis* Meigen, 1818, *A. messeae* Falleroni, 1926, *Culex modestus* Ficalbi, 1890, *C. pipiens* Linnaeus, 1758, *C. torrentium* Martini, 1925, *C. territans* Walker, 1856, *Culiseta fumipennis* (Stephens, 1825), *C. morsitans* (Theobald, 1901), *C. ochroptera* (Peus, 1935), *C. alaskaensis* (Ludlow, 1906), *C. annulata* (Schrank, 1776), *C. bergrothi* (Edwards, 1921), and *Coquillettidia richiardii* (Ficalbi, 1889).

The coordinates of the collection localities of each species were entered in a *.shp file and analyzed using an ArcGIS 10 software. In addition, the file included data on the source of information: our collections, ZIN collection, and literature data. The geographic information system (GIS) is useful for analysis of the records of bloodsucking insect species and description of their geographic distribution. For instance, the mapped species records can be combined with various thematic maps (e.g., climatic ones), containing the original parameters in the given points of the territory or interpolated results based on analysis of the distribution of factors. In this way, the known collection localities of a given species can be used to extrapolate its range boundaries in the region.

Mosquitoes are poikilothermic animals whose metabolism and phenology directly depend on the environmental conditions; therefore, they can exist only within a certain range of environmental factors. In the article, the records of mosquito species were related to a climatic parameter, the sum of active temperatures above

0°C (SAT)[3]. The benefis of using SAT in the study of mosquito distribution had been noted earlier (e.g., Yasyukevich et al., 2017, 2019). Various climatic parameters are considered when predicting the changes in the distribution of agents of transmissible diseases and of their vectors (Pavlovsky, 1964; Korenberg, 1975). In medical entomology and practical epidemiology, thermal parameters are used to control malaria and other diseases in a given territory (Beklemishev et al., 1949; Moshkovsky and Rashina, 1951). The pest control measures in agriculture is determined by the thermal parameters of insect pest development (Popova and Popov, 2013).

In this research we used the free data on the main climatic factors available at the AgroAtlas web site (Afonin et al., 2008) in order to characterize the mosquito distribution in NWR in relation to the environmental parameters. The records of mosquito species close to the northern boundaries of their ranges were compared with the SAT values of the corresponding territories, and the results were used to extrapolate the northern distribution boundaries of 16 species of Culicidae within NWR. We used the SAT values for areas of 100 km^2, obtained from the AgroAtlas web site (Afonin et al., 2008). The SAT values were color coded from green to red (see map legend in Fig. 2).

Below, the records of 16 mosquito species are plotted on the map of NWR with SAT values. The source of information is indicated for each species: our collections, the ZIN material or literature data.

The northernmost records of mosquito species within NWR, including the exact collection localities and their coordinates, were considered in our earlier paper (Khalin and Aibulatov, 2021). The records of mosquitoes from the territories with the minimal SAT values are listed in Table 1. The number of such records given for each species reflects the current level of knowledge of its distribution. A single locality corresponding to the territory with the lowest SAT value is given in some cases: *Anopheles atroparvus*, *Culiseta fumipennis*, and *C. annulata*. For most species, two localities are given, in the western and the eastern parts of NWR. For example, such localities for *Anopheles beklemishevi* are RK in the west and Komi in the east of NWR. For the species whose distribution is somewhat better known, three localities are listed in order to describe the northern range boundary more correctly; for example, the localities of *Anopheles claviger* are SPb (western part), VP (central part), and Komi (eastern part). Some records of species are considered by us to be doubtful; they are marked with asterisks (*) and discussed in the corresponding *Note* sections.

Maps of NWR showing the collection localities of the 16 mosquito species are given below. For each species, the examined material (our collections and the ZIN collection) is listed when present, its distribution in NWR and adjacent territories is characterized, and references to the sources of data are provided. In addition, the distribution of each species outside NWR is briefly described based on the literature data (Gutsevich et al., 1970; Khalin and Gornostaeva, 2008; Becker et al., 2010). The records for Belarus are based on the data of Suslo (2019); those in Europe[4] are based on the data of Robert and co-authors (Robert et al., 2019). The distribution of *Culiseta* species in Russia outside NWR is based on the data of Maslov (1967).

RECORDS OF MOSQUITO SPECIES IN NORTHWESTERN RUSSIA

Anopheles (*Anopheles*) *atroparvus* van Thiel, 1927

Distribution. KP (Levenson et al., 1959) (Fig. 2).

Sweden (Dahl, 1977; Lundström et al., 2013). **Latvia** (Spungis, 2000). **Lithuania** (Pakalniskis et al., 2006).

South of European Russia. Europe (ranging northward to the UK, Belgium, and Denmark); Belarus, Ukraine, Moldova.

Anopheles (*Anopheles*) *beklemishevi* Stegnii et Kabanova, 1976

Distribution (Fig. 2). **RK** (Stegnii et al., 1978; Perevozkin et al., 2012). **LP** (Stegnii et al., 1978; Moskaev

[3] The SAT is the sum of mean daily air temperatures exceeding 0°C for one year.

[4] In the *Distribution* section for each species, we consider under "Europe" the continental and insular parts of Europe outside Russia, excluding Norway, Sweden, Finland, and the former USSR countries.

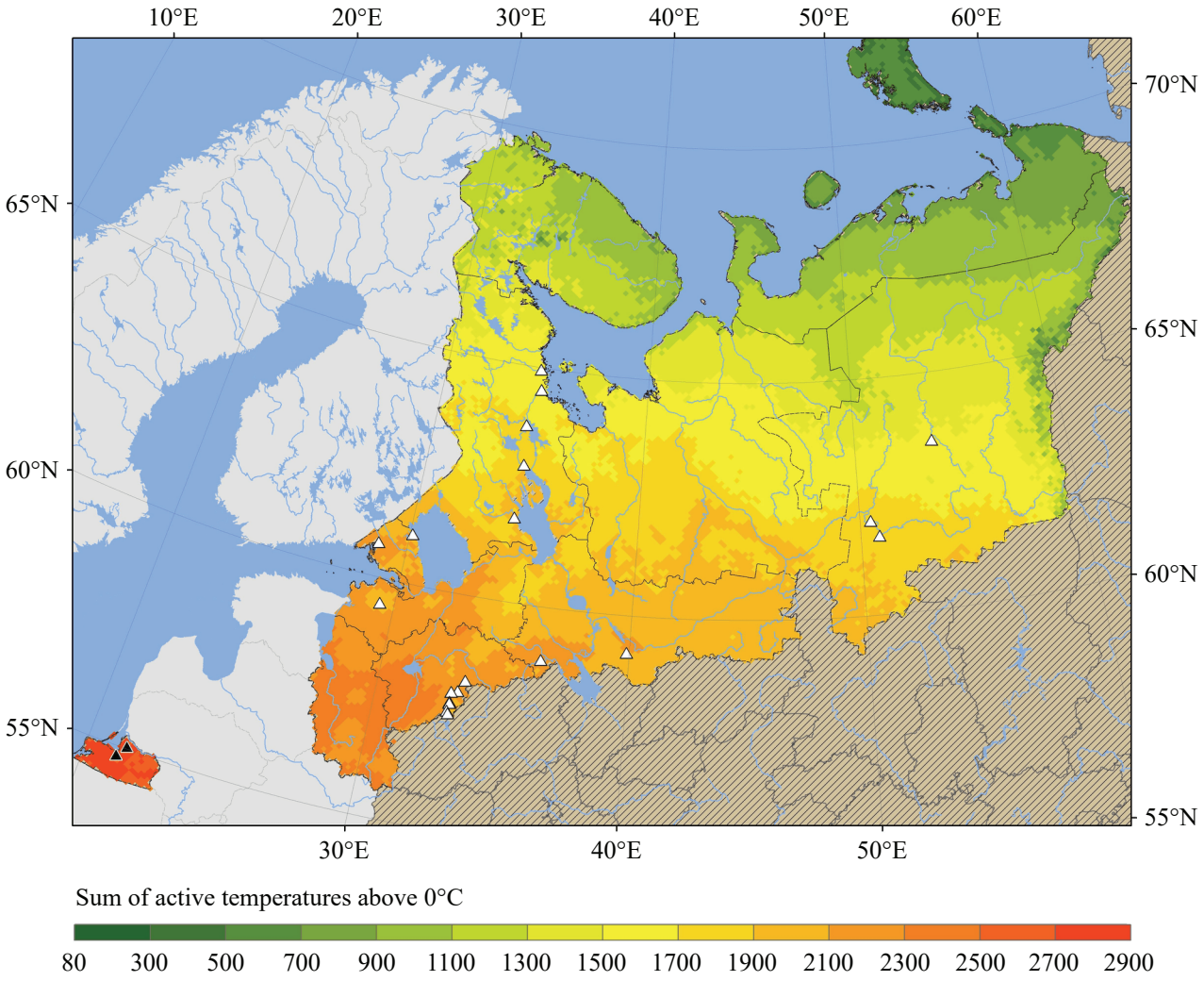

Fig. 2. Collection localities of *Anopheles atroparvus* van Thiel (black triangles) and *A. beklemishevi* Stegnii et Kabanova (white triangles) in Northwestern Russia, according to the literature data. The territories with different values of the sum of active temperatures above 0°C are color coded (see legend).

et al., 2016). **VP** (Belova et al., 2008). **Komi** (Panyukova and Ostroushko, 2017). **NP** (Moskaev et al., 2015).

Sweden (Lundström et al., 2013). **Finland** (Culverwell et al., 2021).

European Russia, Siberia. Sweden, Finland.

Anopheles (*Anopheles*) *claviger* (Meigen, 1804)

Material. SPb, LP, VP (Fig. 3).

Distribution. SPb (Fedorov, 1969). **Komi** (Panyukova and Ostroushko, 2017). **KP** (Levenson et al., 1959). **PP** (Pavlovsky, 1935; Medvedev and Matov, 1999). **NP** (Medvedev and Panyukova, 2005).

Norway (Mehl, 1996). **Sweden** (Dahl, 1975; Schäfer and Lundström, 2001; Lundström et al., 2013; Möhlmann et al., 2017). **Finland** (Utrio, 1977; Culverwell, 2018; Culverwell et al., 2021). **Estonia** (Remm, 1957). **Latvia** (Spungis, 2000). **Lithuania** (Pakalniskis et al., 2006).

European Russia, West Siberia. Europe (ranging northward to the UK, Belgium, and Denmark); North Africa, Belarus, Ukraine, Moldova, Transcaucasia, West and Middle Asia.

Table 1. Records of mosquitoes in Northwestern Russia corresponding to the territories with the lowest values of the sums of active temperatures (SAT) above 0°C

Species	Province / republic, district	Collection locality	Coordinates	SAT, °C	Source of data
Anopheles atroparvus	KP, Slavskii	–	54°03′00.0″N, 21°40′00.0″E	2721.8	Levenson et al., 1959
A. beklemishevi	RK, Belomorskii	Belomorsk	64°31′49.15″N, 34°45′47.98″E	1599.5	Perevozkin et al., 2012
	Komi, Ukhta	Ukhta	63°33′45.45″N, 53°41′2.48″E	1577.2	Panyukova and Ostroushko, 2017
A. claviger	VP, Totemskii	Totma	59°58′24.55″N, 42°45′31.94″E	1989.6	Authors' collections
	Komi, Syktyvkar	Syktyvkar	61°40′7.65″N, 50°50′11.04″E	1863.6	Panyukova and Ostroushko, 2017
A. maculipennis	RK, Kemskii	Kem	64°57′19.92″N, 34°35′54.14″E	1607.3	Perevozkin et al., 2012
	Komi, Ukhta	Ukhta	63°33′45.45″N, 53°41′2.48″E	1577.2	Gordeev and Moskaev, 2014
A. messeae	MP, Pechengskii	Shuioniioki River	69°16′2.06″N, 30°8′24.28″E	1136.4	ZIN collection*
	AP, Arkhangelsk	Arkhangelsk	64°32′23.68″N, 40°30′56.71″E	1659.7	Sharkov, 1982
	Komi, Ukhta	Ukhta	63°33′45.45″N, 53°41′2.48″E	1577.2	Panyukova and Ostroushko, 2017
Culex modestus	NP, Khvoininskii	Khvoinaya	58°54′00.0″N, 34°30′00.0″E	2112.3	Panyukova and Medvedev, 2008
	VP, Vologodskii	–	59°13′13.79″N, 39°53′29.48″E	2124.0	Belova et al., 2008
	LP, Vsevolozhskii	Novosaratovka	59°50′29.5″N, 30°31′32.57″E	2185.7	ZIN collection
C. pipiens	AP, Novaya Zemlya	Belushya Bay	71°30′38.91″N, 52°18′3″E	519.2	Sack, 1923*
	NAO, Zapolyarnyi	Vaygach Island	70°2′10.73″N, 59°28′55.59″E	558.7	de Meijere, 1910*
	MP, Kirovskii	Lake Vudyavr basin	67°37′50.5″N, 33°40′15.2″E	848.3	ZIN collection
	Komi, Vorkuta	Vorkuta	67°29′50.68″N, 64°3′39.93″E	879.0	Panyukova and Ostroushko, 2017
C. torrentium	RK, Kondopozhskii	Kivach	62°16′33.04″N, 33°58′54.59″E	1923.3	Polevoi, 2006
	Komi, Troitsko-Pechorskii	Yaksha	61°49′29.68″N, 56°49′15.96″E	1733.0	Panyukova, 2019
C. territans	Komi, Udorskii	Mezhdurechensk	63°15′00.0″N, 48°33′00.0″E	1587.1	Panyukova and Ostroushko, 2017
	RK, Pryazhinskii	Pryakka	61°41′33.0″N, 33°37′12.0″E	1874.1	ZIN collection

Table 1. (Contd.)

Species	Province / republic, district	Collection locality	Coordinates	SAT, °C	Source of data
Culiseta fumipennis	RK, Medvezhegorskii	Medvezhegorsk	62°18′26.91″N, 35°17′29.44″E	1951.0	Jakovlev et al., 2014
C. morsitans	MP, Kandalakshskii	Kandalaksha	67°9′4.51″N, 32°24′46.16″E	1227.8	ZIN collection
	Komi, Vyktul	Ust-Shchugel	64°16′1.87″N, 57°37′6.86″E	1454.1	Panyukova and Ostroushko, 2017
C. ochroptera	Komi, Sosnogorskii	Nizhnii Odes	63°38′20.12″ N, 54°50′45.02″ E	1490.6	Panyukova and Ostroushko, 2017
	RK, Pryazhinskii	Pryakka	61°41′33.0″N, 33°37′12.0″E	1874.1	ZIN collection
C. alaskaensis	Komi, Vorkuta	Polar Urals	67°0′44.035″N, 65°5′45.614″E	775.5	Beltyukova and Mitrofanova, 1971
	MP, Kirovskii	Lake Vudyavr basin	67°37′50.5″N, 33°40′15.2″E	848.3	ZIN collection
C. annulata	LP, Kingiseppskii	Kurgolovo	59°46′19.3″N, 28°07′49.1″E	2226.4	Authors' collections
C. bergrothi	MP, Kirovskii	Lake Vudyavr basin	67°37′50.5″N, 33°40′15.2″E	848.3	ZIN collection
	Komi, Vorkuta	Vorkuta	67°29′50.68″N, 64°3′39.93″E	879.0	Panyukova and Ostroushko, 2017
Coquillettidia richiardii	RK, Prionezhskii	Pukhta	61°29′55.0″N, 34°39′35.0″E	1966.7	Lobkova, 1956
	Komi, Priluzskii	Prislon	59°36′30.0″N, 49°25′20.0″E	2021.6	Panyukova and Ostroushko, 2017

Dash indicates that the exact locality was not specified in the literature; in such cases the coordinates of the district center are given.

Anopheles (*Anopheles*) *maculipennis* Meigen, 1818 sensu stricto[5]

Distribution (Fig. 4). **RK** (Perevozkin et al., 2012; Jakovlev et al., 2014). **LP** (Stegnii et al., 1978; Moskaev et al., 2016). **Komi** (Gordeev and Moskaev, 2014; Panyukova and Ostroushko, 2017). **NP** (Moskaev et al., 2015). **KP** (Levenson et al., 1959; Bernotiene, 2012; Perevozkin et al., 2018).

Sweden (Dahl, 1977; Lundström et al., 2013; Möhlmann et al., 2017). **Finland** (Utrio, 1977; Culverwell, 2018; Culverwell et al., 2021). **Latvia** (Spungis, 2000). **Lithuania** (Pakalniskis et al., 2006).

European Russia, West Siberia. Europe (ranging northward to the UK, Belgium, and Denmark); North Africa, Belarus, Ukraine, Moldova, Transcaucasia, West and Middle Asia.

Anopheles (*Anopheles*) *messeae* Falleroni, 1926

Material. MP* (Fig. 5).

Distribution. AP (Sharkov, 1982). **RK** (Lobkova, 1956; Stegnii et al., 1978; Perevozkin et al., 2012). **SPb** (Fedorov, 1969; Stegnii et al., 1978). **LP** (Stegnii et al.,

[5] *Anopheles maculipennis* is considered here as a single species and not as a species complex. Identification of species in this complex requires special techniques, whereas *A. maculipennis* sensu lato can be diagnosed by distinct larval and adult morphological characters. Correspondingly, here we give references only to those publications in which the material was identified not to *A. maculipennis* s. l. but to individual species.

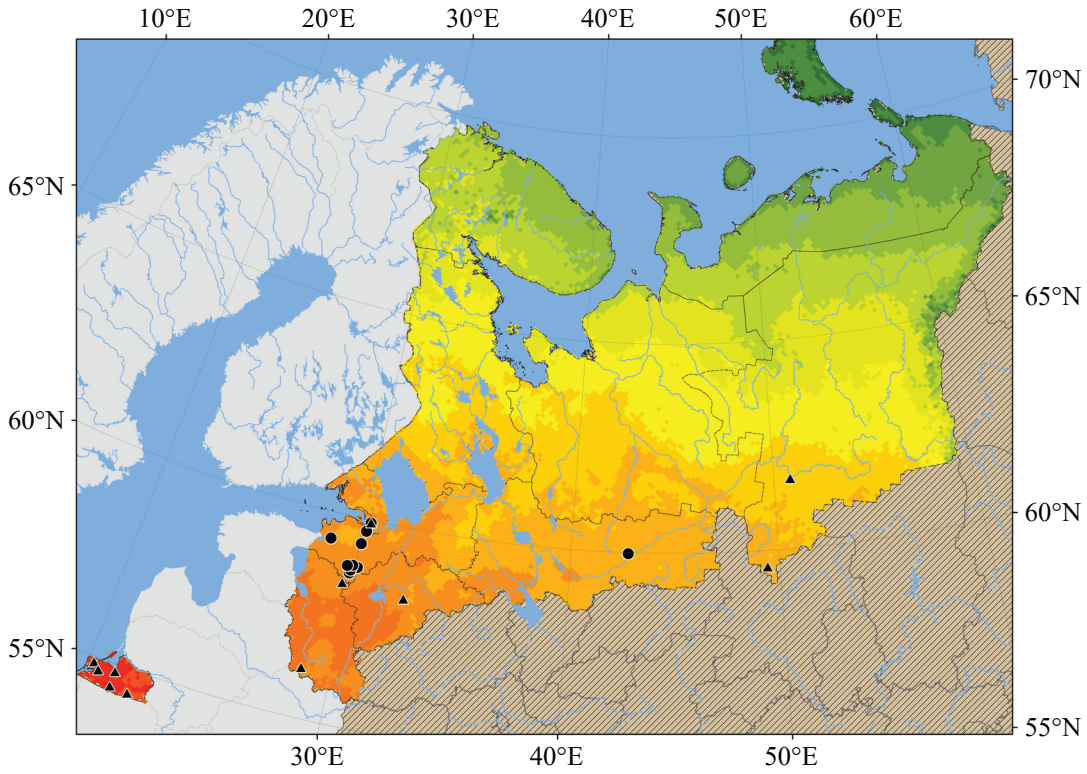

Fig. 3. Collection localities of *Anopheles claviger* (Meigen) in Northwestern Russia, according to the collection material (circles) and the literature data (triangles).

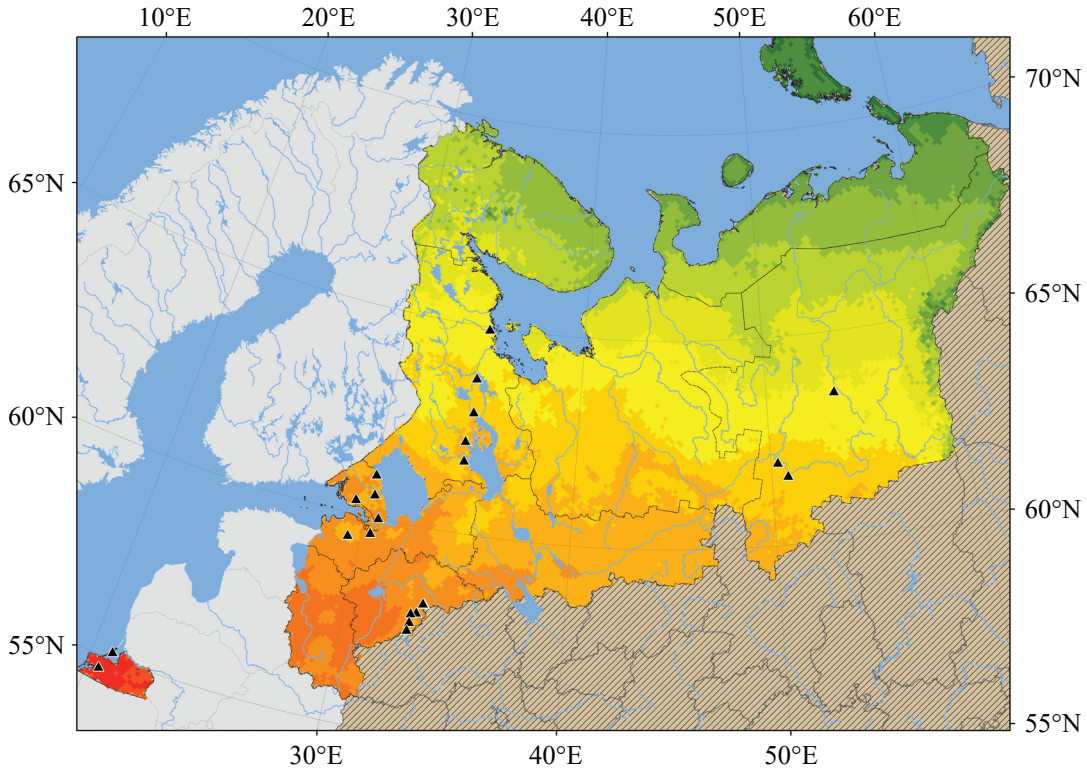

Fig. 4. Collection localities of *Anopheles maculipennis* Meigen in Northwestern Russia. Designations as in Fig. 3.

1978; Moskaev et al., 2016). **VP** (Sharkov, 1982; Belova et al., 2008). **Komi** (Ostroushko, 1986; Panyukova and Ostroushko, 2017). **PP** (Chetverikova, 2014). **NP** (Moskaev et al., 2015). **KP** (Levenson et al., 1959; Perevozkin et al., 2018).

Norway (Mehl, 1996). **Sweden** (Dahl, 1977; Lundström et al., 2013). **Finland** (Utrio, 1977; Culverwell, 2018; Culverwell et al., 2021). **Latvia** (Spungis, 2000). **Lithuania** (Pakalniskis et al., 2006).

European Russia, Siberia. Europe (ranging northward to the UK, Belgium, and Denmark); Belarus, Ukraine, Moldova, Middle Asia, Northeast China.

Note. The only specimen studied by us is a head preparation of a female mosquito identified earlier by A.V. Gutsevich. We cannot confirm this identification. It is possible that the female was reared from an egg identified as *Anopheles messeae*.

Culex (*Barraudius*) *modestus* Ficalbi, 1890

Material. SPb, LP (Fig. 6).

Distribution. VP (Belova et al., 2008). **PP** (Medvedev and Matov, 1999). **NP** (Panyukova and Medvedev, 2008).

Sweden (Möhlmann et al., 2017).

European Russia, Siberia, the Russian Far East. Europe (ranging northward to the UK, the Netherlands, and Denmark); North Africa, Belarus, Ukraine, Moldova, Transcaucasia, West, Middle, and South Asia.

Culex (*Culex*) *pipiens* Linnaeus, 1758

Material. MP, RK, SPb, LP, KP, PP, NP (Fig. 7).

Distribution. MP (Shub and Nikolaev, 1937; Lobkova, 1964; Tamarina and Aleksandrova, 1974; Sharkov, 1976). **AP*** (Sack, 1923). **NAO*** (de Meijere, 1910). **RK** (Shingareva, 1926; Shub and Nikolaev, 1937; Lobkova, 1956, 1980; Lobkova and Makarova, 1961; Sharkov et al., 1984; Polevoi, 2006). **SPb** (Osten-Sacken, 1858; Fedorov, 1946, 1969; Gutsevich, 1948). **VP** (Adrianov, 1953; Ozerov, 1957; Sharkov, 1982; Belova et al., 2008). **Komi** (Shub and Nikolaev, 1937; Ostroushko, 1986; Panyukova and Ostroushko, 2017). **KP** (Levenson et al., 1959; Bernotiene, 2012). **PP** (Medvedev and Matov, 1999; Chetverikova, 2014). **NP** (Fedorova, 1977; Kunkova, 2000; Panyukova and Medvedev, 2008).

Norway (Natvig, 1948; Mehl, 1996). **Sweden** (Natvig, 1948; Dahl, 1975; Schäfer and Lundström, 2001; Lundström et al., 2013; Hesson et al., 2015; Möhlmann et al., 2017). **Finland** (Natvig, 1948; Utrio, 1977; Culverwell, 2018; Culverwell et al., 2021). **Estonia** (Remm, 1957). **Latvia** (Spungis, 2000). **Lithuania** (Pakalniskis et al., 2006).

European Russia, Siberia, the Russian Far East. Europe (ranging northward to the UK, Belgium, and Denmark); North Africa, Belarus, Ukraine, Moldova, West and Middle Asia. Holarctic (excluding most transpolar regions), locally in the Ethiopian, Neotropical, and Australian regions.

Note. The records of *Culex pipiens* from AP [the Novaya Zemlya Archipelago, Belushya Bay (Sack, 1923)] and NAO [Zapolyarnyi District, Vaygach Island (de Meijere, 1910)] were probably based on misidentification. The other records are located far southward from the Novaya Zemlya and Vaygach Island (Table 1; Fig. 7), including those outside Russia, in Sweden: Norrbotten, 67°08′09.0″N, 18°30′03.5″E (Lundström et al., 2013) and Haparanda, 65°49′60.0″N, 24°07′60.0″E (Hesson et al., 2015); in Finland: Lahti, 60°58′60.0″N, 25°39′20.0″E (Hesson et al., 2015) and Larsmo, 63°45′N, 22°48′E (Natvig, 1948).

Culex (*Culex*) *torrentium* Martini, 1925

Material. SPb, LP, NP (Fig. 8).

Distribution. RK (Polevoi, 2006). **SPb** (Fedorov, 1969). **VP** (Belova et al., 2008). **Komi** (Panyukova, 2019). **PP** (Chetverikova, 2014). **NP** (Kunkova and Fedorova, 2003; Panyukova and Medvedev, 2008).

Norway (Mehl, 1996). **Sweden** (Schäfer and Lundström, 2001; Lundström et al., 2013; Hesson et al., 2015). **Finland** (Utrio, 1977; Culverwell, 2018; Culverwell et al., 2021). **Estonia** (Remm, 1957). **Lithuania** (Pakalniskis et al., 2006).

European Russia, West Siberia. Europe (ranging northward to the UK, Belgium, and Denmark); Belarus, Moldova, West Asia.

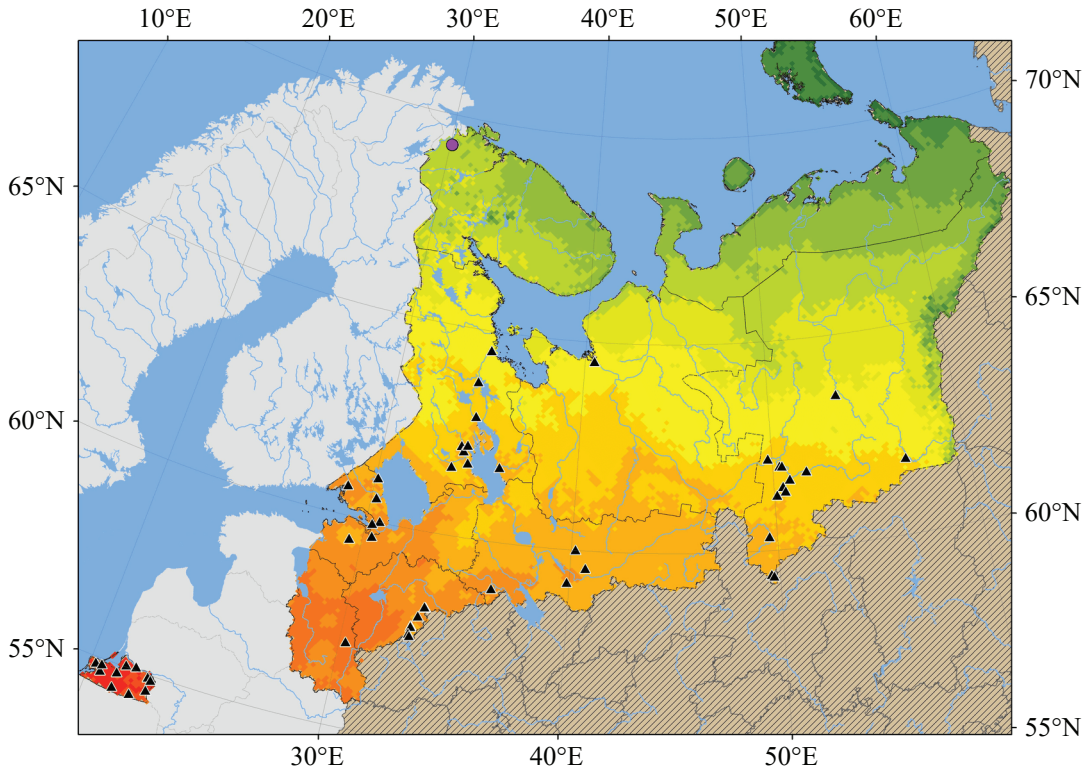

Fig. 5. Collection localities of *Anopheles messeae* Falleroni in Northwestern Russia. Designations as in Fig. 3. The location with doubtful species identification is shown in purple.

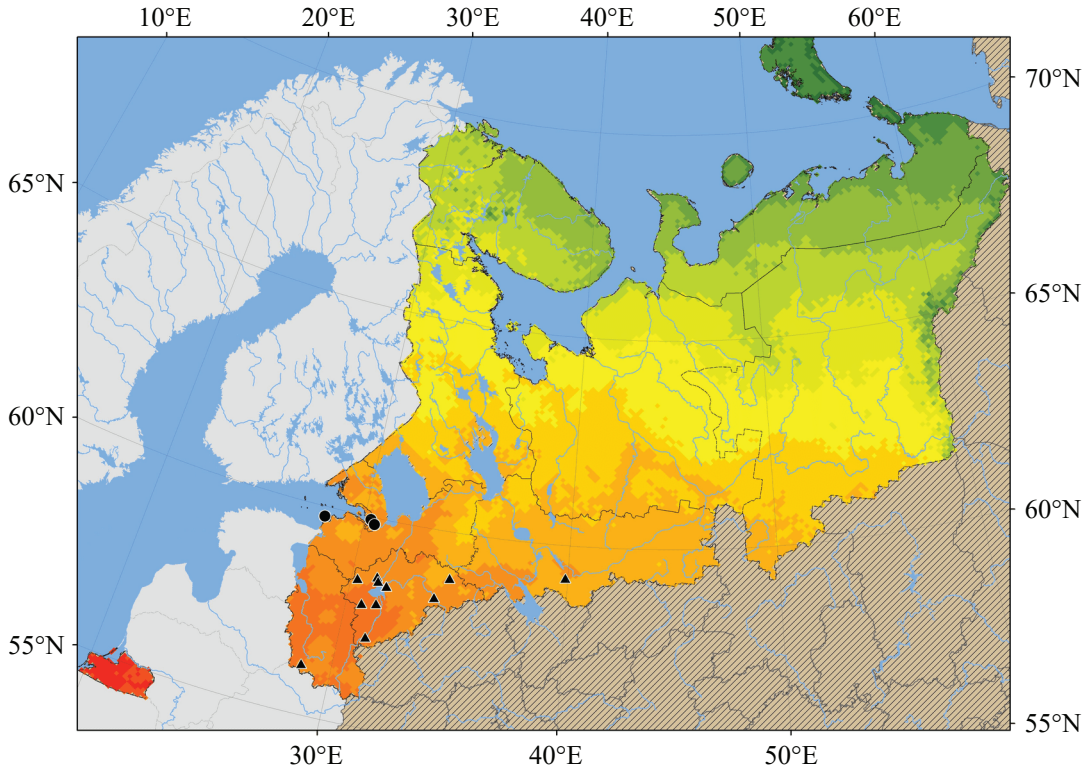

Fig. 6. Collection localities of *Culex modestus* Ficalbi in Northwestern Russia. Designations as in Fig. 3.

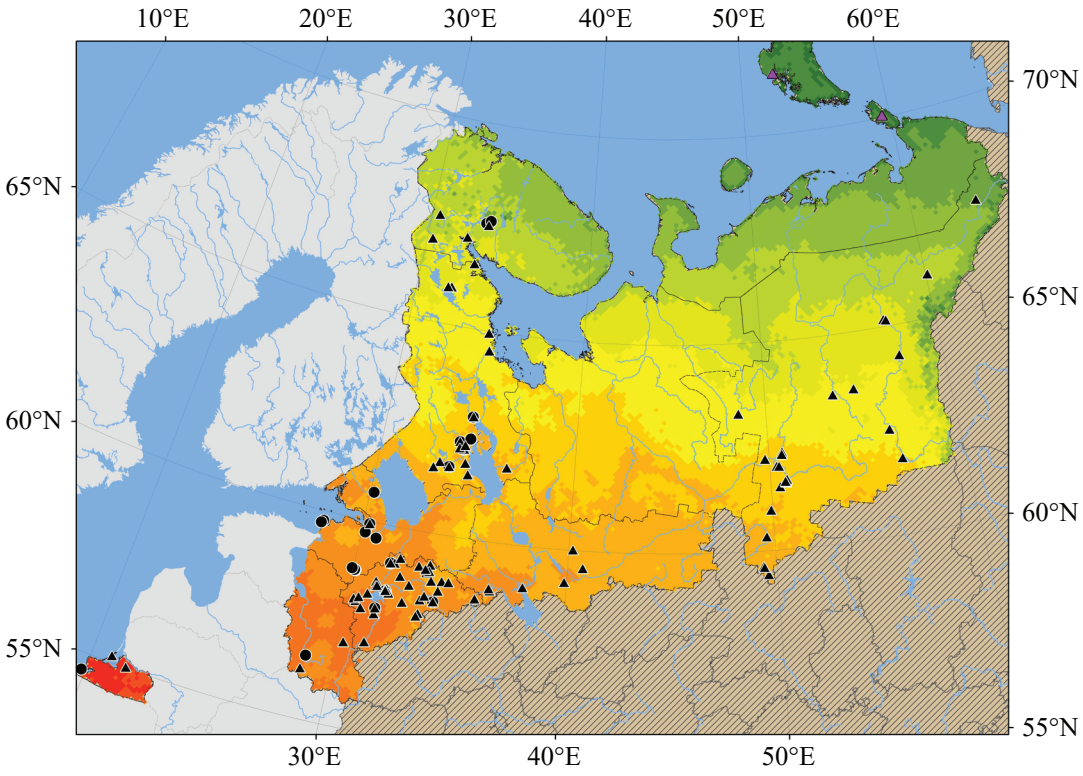

Fig. 7. Collection localities of *Culex pipiens* Linnaeus in Northwestern Russia. Designations as in Figs. 3, 5.

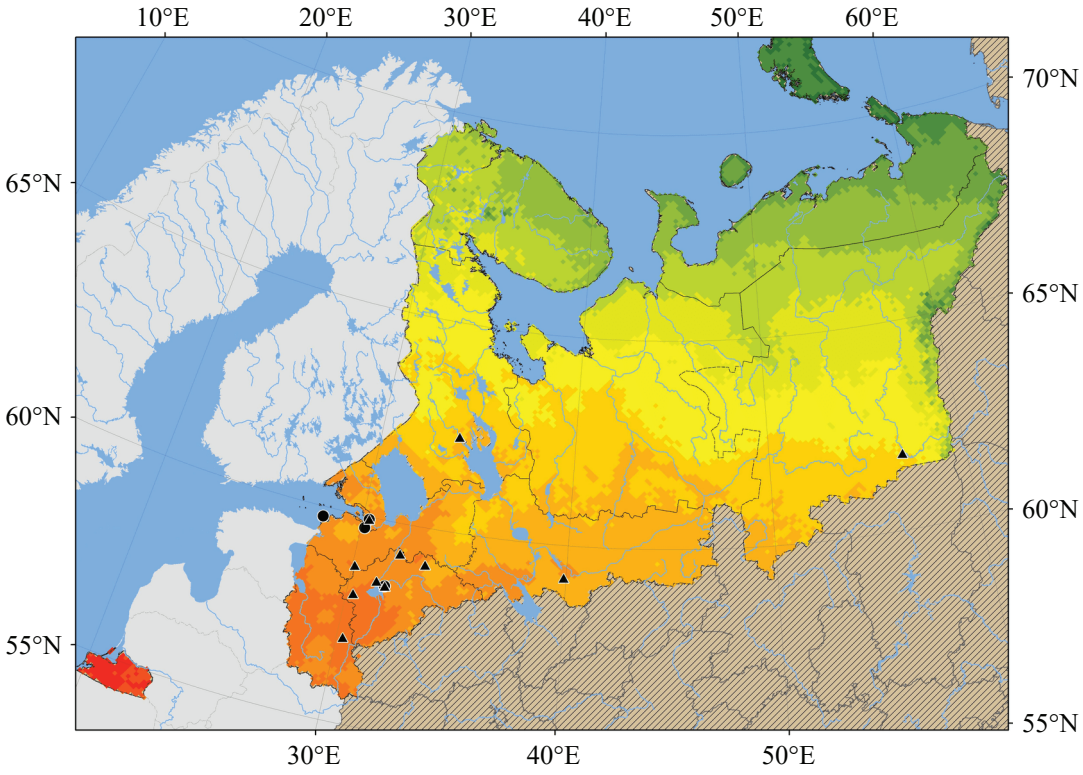

Fig. 8. Collection localities of *Culex torrentium* Martini in Northwestern Russia. Designations as in Fig. 3.

Culex* (*Neoculex*) *territans Walker, 1856

Material. RK, SPb, LP, NP (Fig. 9).

Distribution. RK (Lobkova, 1964; Jakovlev et al., 2014). **SPb** (Fedorov, 1969). **VP** (Belova et al., 2008). **Komi** (Panyukova and Ostroushko, 2017). **PP** (Medvedev and Matov, 1999). **NP** (Panyukova and Medvedev, 2008).

Norway (Natvig, 1948; Mehl, 1996). **Sweden** (Natvig, 1948; Schäfer and Lundström, 2001; Lundström et al., 2013). **Finland** (Natvig, 1948; Utrio, 1977; Culverwell, 2018; Culverwell et al., 2021). **Estonia** (Remm, 1957). **Lithuania** (Pakalniskis et al., 2006).

European Russia, Siberia, the Russian Far East. Europe (ranging northward to the UK, Belgium, and Denmark); North Africa, Belarus, Moldova, West and Middle Asia; North America.

Culiseta* (*Culisella*) *fumipennis
(Stephens, 1825)

Material. RK, SPb, LP (Fig. 10).

Distribution. RK (Humala and Polevoi, 2009; Jakovlev et al., 2014). **SPb** (Gutsevich, 1948).

Norway (Natvig, 1948; Mehl, 1996). **Sweden** (Natvig, 1948; Schäfer and Lundström, 2001; Lundström et al., 2013). **Estonia** (Remm, 1957).

European Russia (north and west), south of West Siberia. Europe (ranging northward to the UK, Belgium, and Denmark); North Africa, Belarus, Ukraine, West Asia.

Culiseta* (*Culisella*) *morsitans
(Theobald, 1901)

Material. MP, RK, SPb, LP, PP (Fig. 11).

Distribution. RK (Lobkova, 1964, 1965). **SPb** (Gutsevich, 1948; Fedorov, 1969). **Komi** (Ostroushko, 1986; Panyukova and Ostroushko, 2017). **KP** (Bernotiene, 2012). **PP** (Medvedev and Matov, 1999). **NP** (Panyukova and Medvedev, 2008).

Norway (Natvig, 1948; Mehl, 1996). **Sweden** (Natvig, 1948; Schäfer and Lundström, 2001; Lundström et al., 2013; Hesson et al., 2015; Möhlmann et al., 2017). **Finland** (Natvig, 1948; Utrio, 1977; Culverwell, 2018; Culverwell et al., 2021). **Estonia** (Remm, 1957). **Lithuania** (Pakalniskis et al., 2006).

European Russia (northwest, west, center), south of West Siberia. Europe (ranging northward to the UK, Belgium, and Denmark); North Africa, Belarus, Ukraine, West Asia.

Culiseta* (*Culisella*) *ochroptera (Peus, 1935)

Material. RK, SPb, LP (Fig. 12).

Distribution. AP (Shevkunova and Gracheva, 1961). **RK** (Polevoi, 2006; Jakovlev et al., 2014). **SPb** (Fedorov, 1946, 1969). **Komi** (Panyukova and Ostroushko, 2017). **KP** (Bernotiene, 2012). **NP** (Panyukova and Medvedev, 2008).

Norway (Mehl, 1996). **Sweden** (Schäfer and Lundström, 2001; Lundström et al., 2013; Möhlmann et al., 2017). **Finland** (Utrio, 1977; Culverwell et al., 2021). **Estonia** (Remm, 1957). **Lithuania** (Pakalniskis et al., 2006).

European Russia, West Siberia, the Russian Far East. Europe (ranging northward to the Netherlands and Germany); Belarus, Ukraine, Northeast China.

Note. Shevkunova and Gracheva (1961) reported *Culiseta ochroptera* from AP but did not specify the exact collection locality. Since AP is a vast territory, we have not mapped this record in Fig. 12.

Culiseta* (*Culiseta*) *alaskaensis
(Ludlow, 1906)

Material. MP, RK, SPb, LP, Komi (Fig. 13).

Distribution. MP (Shingareva, 1926; Gutsevich, 1934; Solovei and Likhoded, 1966; Tamarina and Aleksandrova, 1974; Sharkov, 1976, 1980a). **AP** (Edwards, 1921; Stackelberg, 1937; Sharkov, 1982). **NAO** (Monchadsky, 1950). **RK** (Shingareva, 1926; Natvig, 1948; Lobkova, 1956; Lobkova and Makarova, 1961; Jakovlev et al., 2014). **SPb** (Gutsevich, 1948; Fedorov, 1969). **LP** (Natvig, 1948; Taldrik, 1967). **VP** (Adrianov, 1953; Sharkov, 1982; Belova et al., 2008). **Komi** (Belokur, 1960; Beltyukova and Mitrofanova, 1971; Bryushinina, 1971; Potapov et al., 1972; Ostroushko, 1986; Panyukova and Ostroushko, 2017). **KP** (Bernotiene, 2012). **PP** (Medvedev and Matov, 1999). **NP** (Panyukova and Medvedev, 2008).

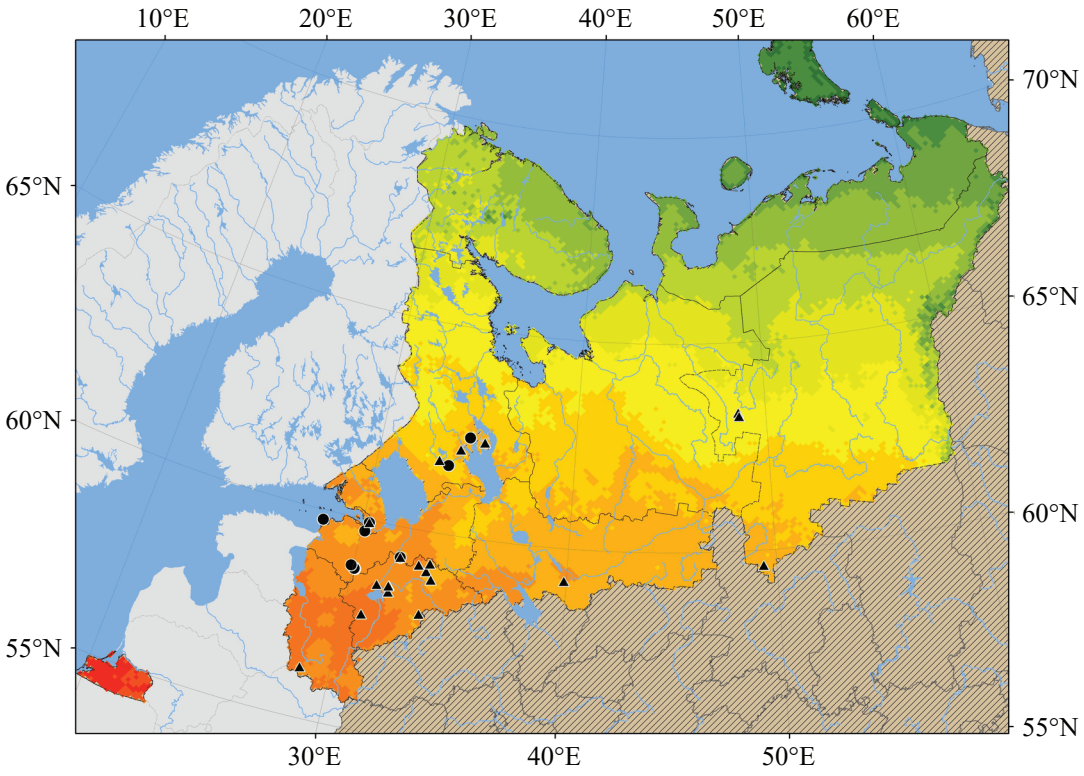

Fig. 9. Collection localities of *Culex territans* Walker in Northwestern Russia. Designations as in Fig. 3.

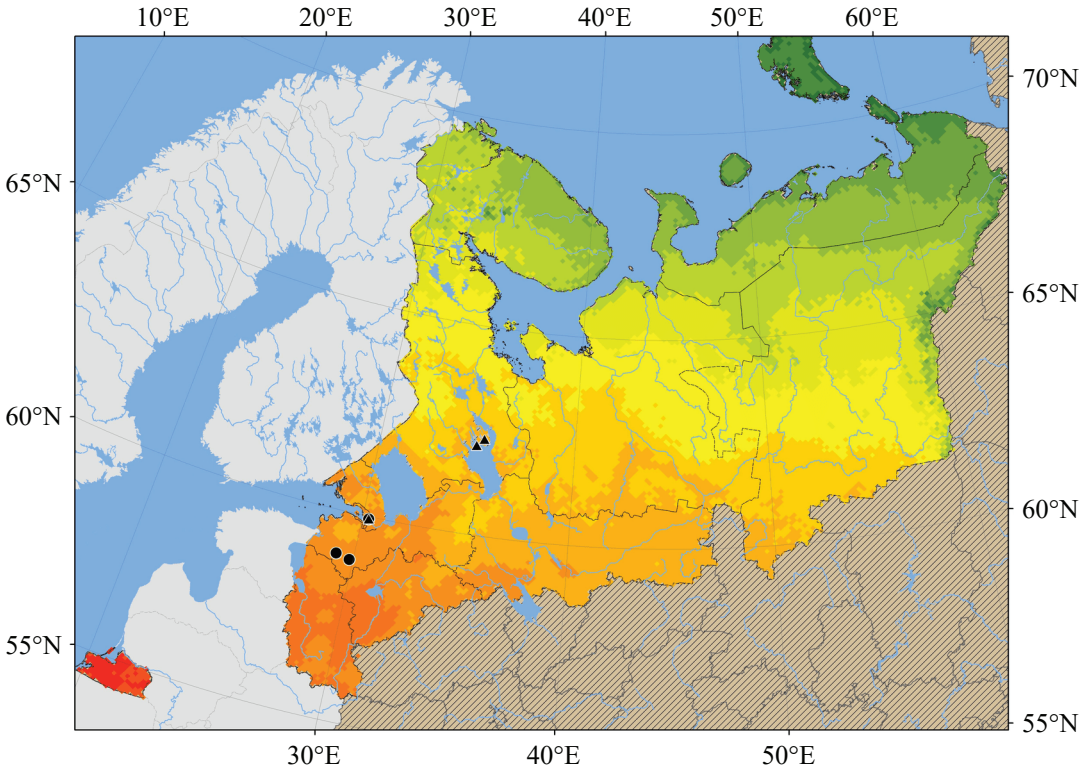

Fig. 10. Collection localities of *Culiseta fumipennis* (Stephens) in Northwestern Russia. Designations as in Fig. 3.

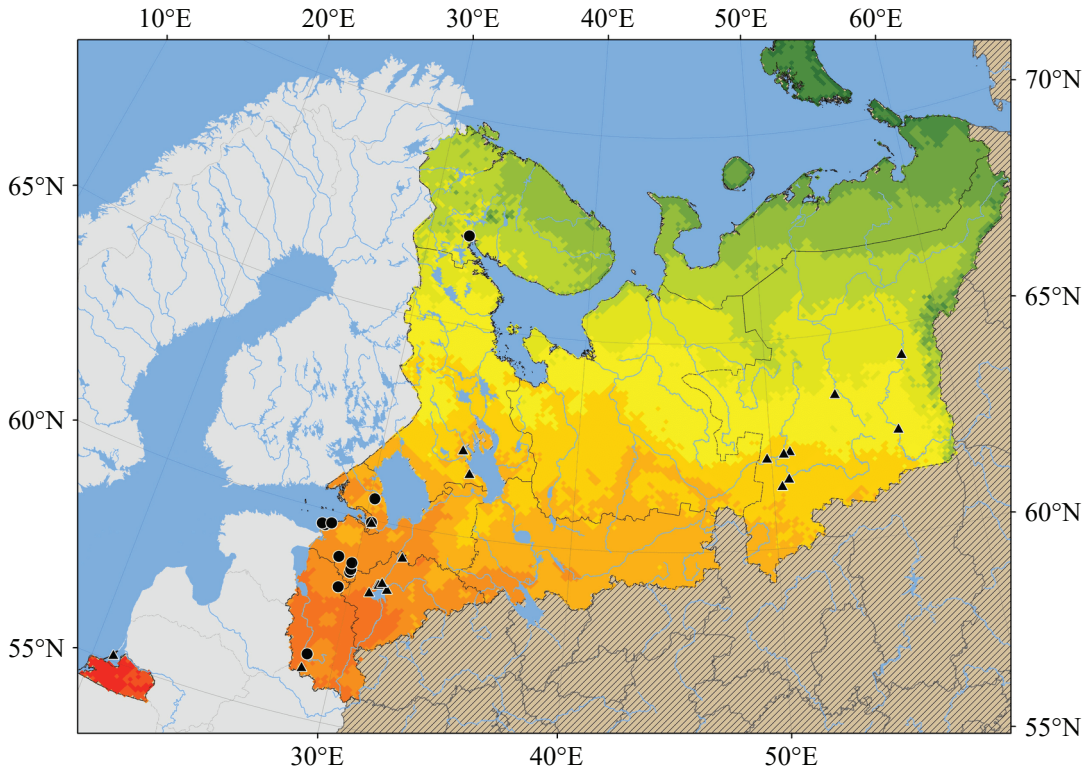

Fig. 11. Collection localities of *Culiseta morsitans* (Theobald) in Northwestern Russia. Designations as in Fig. 3.

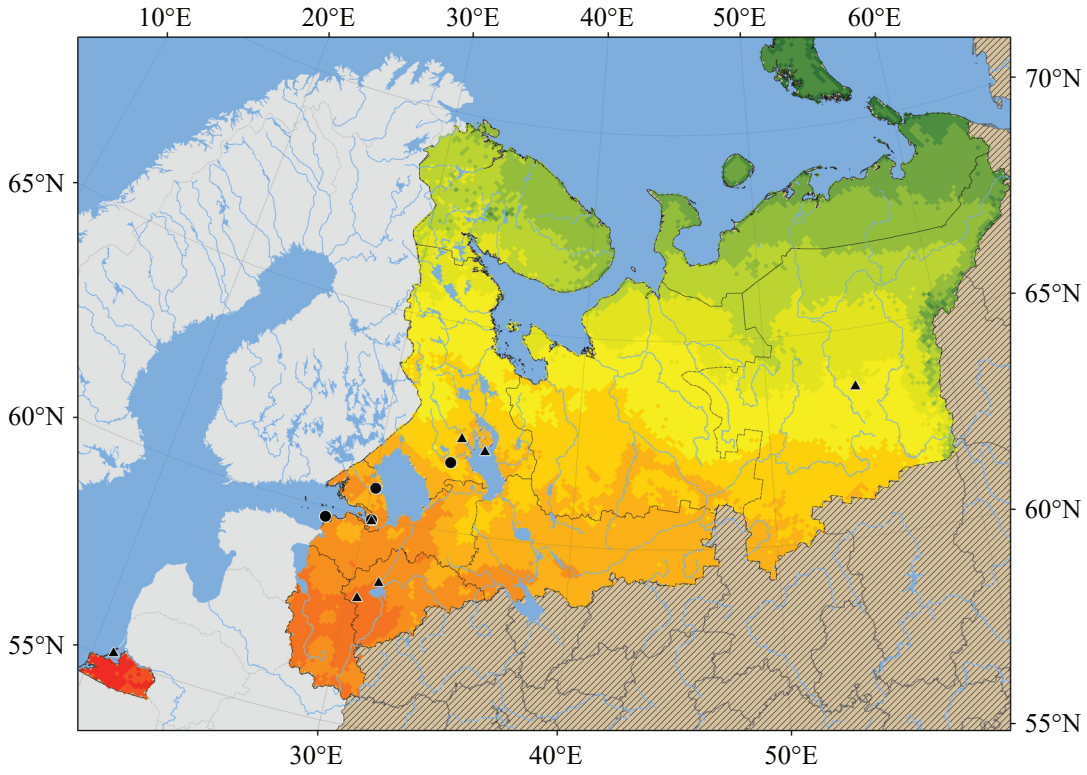

Fig. 12. Collection localities of *Culiseta ochroptera* (Peus) in Northwestern Russia. Designations as in Fig. 3.

Norway (Natvig, 1948; Mehl, 1996). **Sweden** (Natvig, 1948; Schäfer and Lundström, 2001; Lundström et al., 2013; Möhlmann et al., 2017). **Finland** (Natvig, 1948; Utrio, 1977; Culverwell, 2018; Culverwell et al., 2021). **Estonia** (Remm, 1957). **Latvia** (Spungis, 2000). **Lithuania** (Pakalniskis et al., 2006).

European Russia, Siberia, the Russian Far East. Europe (ranging northward to the UK and the Netherlands); Belarus, Ukraine, Moldova; North America.

Culiseta (*Culiseta*) *annulata* (Schrank, 1776)

Material. SPb, LP, KP (Fig. 14).

Distribution. SPb (Gutsevich, 1948; Fedorov, 1969). **PP** (Medvedev and Matov, 1999). NP (Panyukova and Medvedev, 2008).

Norway (Natvig, 1948; Mehl, 1996). **Sweden** (Natvig, 1948; Dahl, 1975; Schäfer and Lundström, 2001; Lundström et al., 2013; Möhlmann et al., 2017). **Finland** (Utrio, 1977; Culverwell, 2018; Culverwell et al., 2021). **Estonia** (Remm, 1957). **Latvia** (Spungis, 2000). **Lithuania** (Pakalniskis et al., 2006).

European Russia (west and northwest), Siberia, the Russian Far East. Europe (ranging northward to the UK, Belgium, and Denmark); North Africa, Belarus, Ukraine, Moldova, Transcaucasia, Asia Minor, Kazakhstan, Middle Asia.

Culiseta (*Culiseta*) *bergrothi* (Edwards, 1921)

Material. MP, RK, SPb, LP, Estonia (Fig. 15).

Distribution. MP (Shingareva, 1926; Stackelberg, 1937; Rumsh, 1948; Solovei and Likhoded, 1966; Tamarina and Aleksandrova, 1974; Sharkov, 1980a, 1980b). **AP** (Sharkov, 1982). **RK** (Lobkova, 1956; Jakovlev et al., 2014). **VP** (Sharkov, 1982; Belova et al., 2008). **Komi** (Ostroushko, 1986; Panyukova and Ostroushko, 2017). **PP** (Medvedev and Matov, 1999).

Norway (Natvig, 1948; Mehl, 1996). **Sweden** (Natvig, 1948; Schäfer and Lundström, 2001; Lundström et al., 2013; Möhlmann et al., 2017). **Finland** (Natvig, 1948; Utrio, 1977; Culverwell et al., 2021). **Estonia** (Maslov, 1967).

European Russia (north and west), Siberia, the Russian Far East. Europe (Denmark), Kazakhstan, Mongolia, North China, Korea, Japan.

Coquillettidia richiardii (Ficalbi, 1889)

Material. RK, SPb, LP, PP, NP (Fig. 16).

Distribution. RK (Lobkova, 1956; Jakovlev et al., 2014). **SPb** (Gutsevich, 1948; Fedorov, 1969). **LP** (Taldrik, 1967). **Komi** (Panyukova and Ostroushko, 2017). **KP** (Levenson et al., 1959; Bernotiene, 2012). **PP** (Medvedev and Matov, 1999). **NP** (Fedorova, 1977; Panyukova and Medvedev, 2008).

Norway (Mehl, 1996). **Sweden** (Natvig, 1948; Schäfer and Lundström, 2001; Lundström et al., 2013; Möhlmann et al., 2017). **Finland** (Natvig, 1948; Utrio, 1977; Culverwell, 2018; Culverwell et al., 2020). **Estonia** (Remm, 1957). **Latvia** (Spungis, 2000). **Lithuania** (Pakalniskis et al., 2006).

European Russia, West Siberia. Europe (ranging northward to the UK, Belgium, and Denmark); North Africa, Belarus, Ukraine, Moldova, Asia Minor, Kazakhstan, Middle Asia.

DISCUSSION

Analysis of additional publications has allowed us to correct the mosquito check-list in NWR, currently comprising 47 species; the list was supplemented with *Anopheles atroparvus*, recorded in KP (Levenson et al., 1959). In the course of the examination of the records of species of the genera *Anopheles*, *Coquillettidia*, *Culex*, and *Culiseta* in comparison with the SAT parameter, the minimal SAT values for each species within NWR were determined (Table 2) and the position of the northern range boundaries of these species was analyzed. Based on our material and the ZIN collections, the northern distribution boundaries in NWR were updated for five species: *Anopheles claviger*, *A. messeae*, *Culiseta morsitans*, *Culex territans*, and *C. modestus*. Based on the minimal SAT values, species of the genera *Anopheles*, *Coquillettidia*, *Culex*, and *Culiseta* were included in four groups (Fig. 17).

Group 1. Three species: *Culex pipiens*, *Culiseta alaskaensis*, and *C. bergrothi*. These species are distributed in the area with SAT values exceeding 770°C (i.e., the whole territory of NWR excluding the north and east of

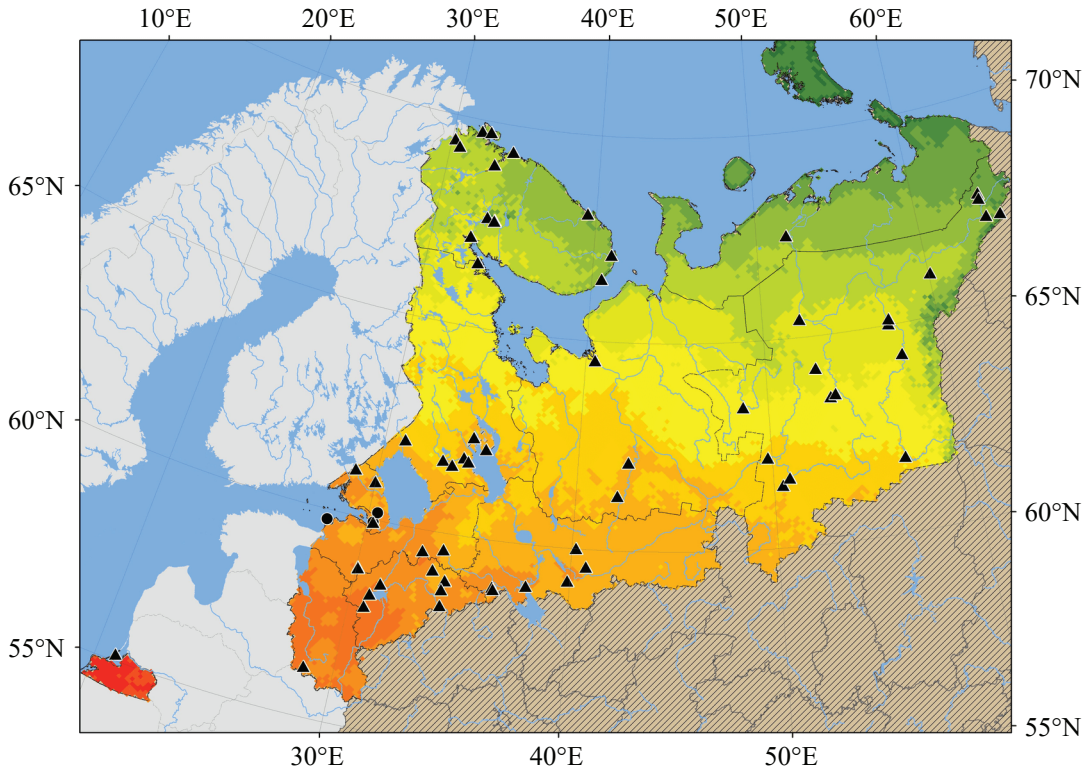

Fig. 13. Collection localities of *Culiseta alaskaensis* (Ludlow) in Northwestern Russia. Designations as in Fig. 3.

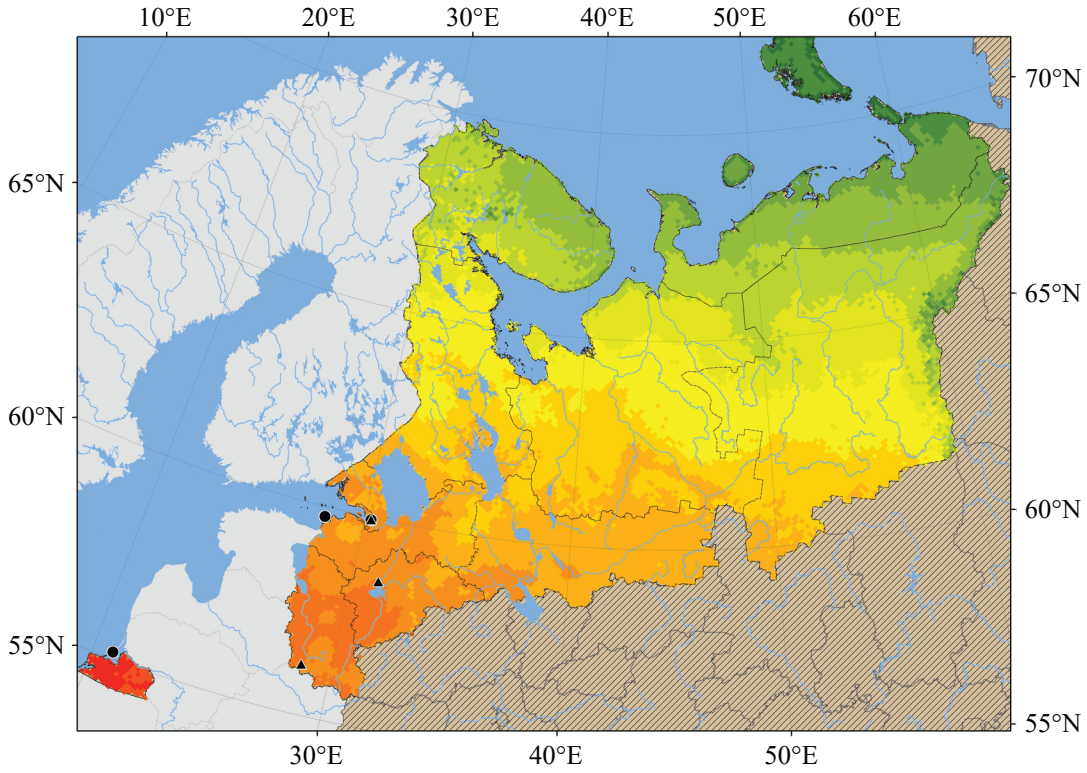

Fig. 14. Collection localities of *Culiseta annulata* (Schrank) in Northwestern Russia. Designations as in Fig. 3.

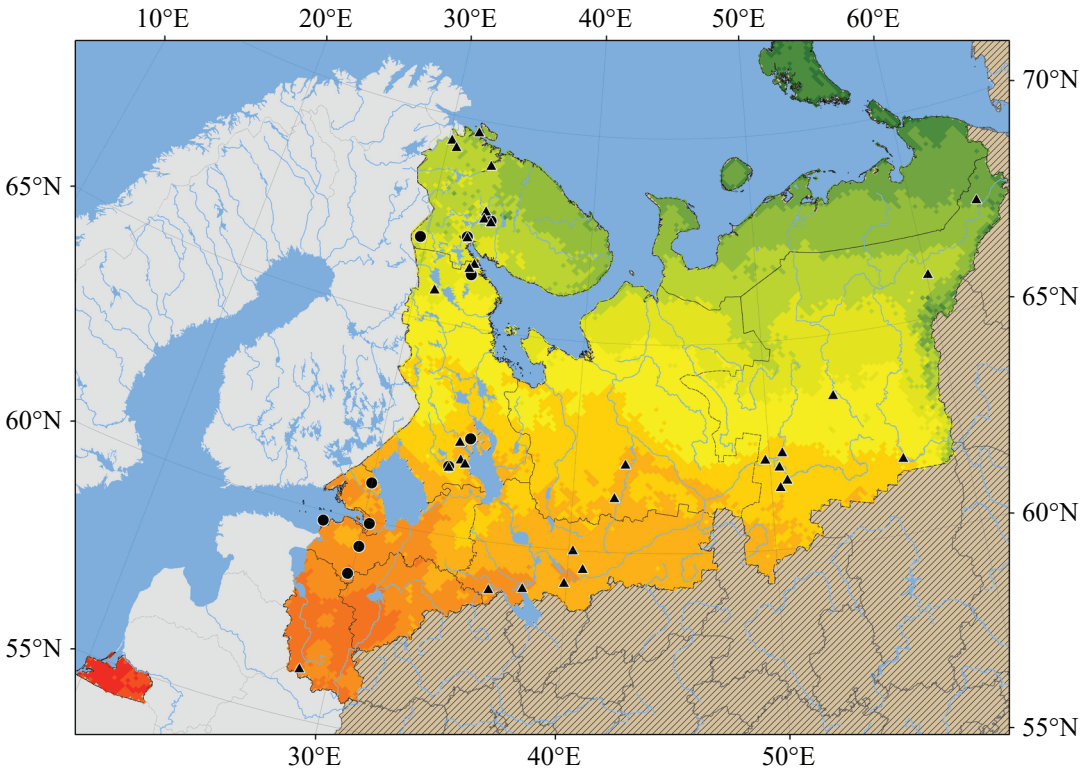

Fig. 15. Collection localities of *Culiseta bergrothi* (Edwards) in Northwestern Russia. Designations as in Fig. 3.

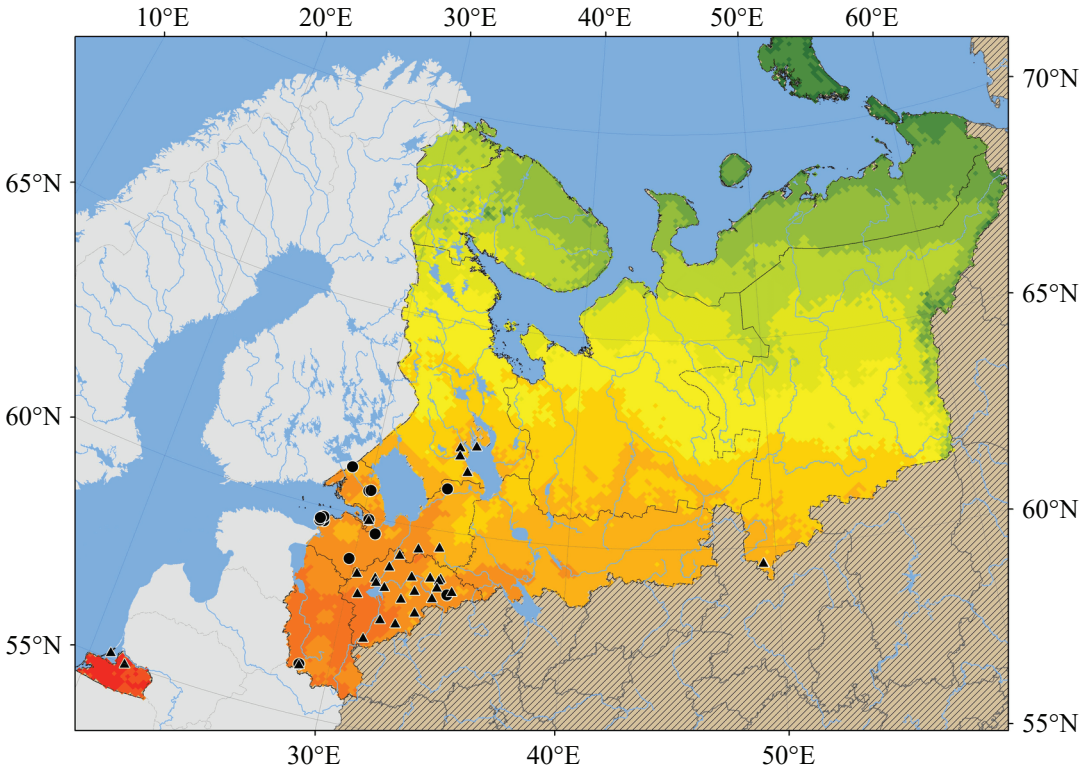

Fig. 16. Collection localities of *Coquillettidia richiardii* (Ficalbi) in Northwestern Russia. Designations as in Fig. 3.

Table 2. Minimal values of the sums of active temperatures above 0°C for mosquito species in Northwestern Russia

Species	Min SAT, °C	Group
Culiseta alaskaensis	775.5	1
C. bergrothi	848.3	
Culex pipiens	848.3	
Culiseta morsitans	1227.8	2
C. ochroptera	1490.6	
Anopheles beklemishevi	1577.2	
A. maculipennis	1577.2	
A. messeae	1577.2	
Culex territans	1587.1	
Culex torrentium	1733.2	3
Anopheles claviger	1863.6	
Culiseta fumipennis	1951.0	
Coquillettidia richiardii	1966.7	
Culex modestus	2112.3	4
Culiseta annulata	2226.4	
Anopheles atroparvus	2721.8	

Each group includes all the species of the former group, i.e., group 2 includes group 1; group 3 includes groups 1 and 2; group 4 comprises all the 16 mosquito species.

NAO and the insular part of AP; see Fig. 17). No species of the genera *Anopheles*, *Coquillettidia*, *Culex*, and *Culiseta* have been reliably recorded in the territories of NWR with SAT values below 770°C.

Group 2. Nine species, including 3 species of group 1 and also *Anopheles beklemishevi*, *A. maculipennis*, *A. messeae*, *Culex territans*, *Culiseta morsitans*, and *C. ochroptera*. These species are distributed in the area with SAT values exceeding 1227°C (i.e., the territory of NWR excluding the greatest parts of MP and NAO and the north and east of the Komi Republic; see Fig. 17). The northernmost locality of *Culiseta morsitans* differs considerably from those of the remaining species in a lower SAT value (see Table 2). The records with SAT 1577.2°C are probably located near the northern distribution boundary of Anophelinae mosquitoes in NWR; as compared with this value, the record of an *Anopheles* mosquito in MP (Shuioniioki River, SAT 1136.4°C) is quite unexpected.

Group 3. Thirteen species: all the examined species excluding *Anopheles atroparvus*, *Culex modestus*, and *Culiseta annulata*. Mosquitoes of this group are distributed in the area with SAT values exceeding 1733°C (KP, LP, south of RK, AP, Komi, VP, PP, and NP). *Coquillettidia richiardii* is the only species of its genus in the North Palaearctic; correspondingly, the locality with a SAT value of 1966.7°C probably lies at the northern distribution boundary of the genus *Coquillettidia* in NWR.

Group 4. Sixteen species: all the species studied here. They are distributed in the area with SAT values exceeding 2112°C: KP, south and west of LP, PP, most of NP, and south of VP. For instance, *Culex modestus* was found in the south of VP (SAT 2112.3°C and higher), and *Culiseta annulata* was recorded in SPb (SAT over 2226.4°C). *Anopheles atroparvus* was the most thermophilous of all the 16 species in the NWR fauna: it was found only in the west of KP (SAT over 2721.8°C).

Mosquitoes are amphibiotic insects whose larvae and pupae develop in temporary and permanent water bodies, while the adults are terrestrial. The larvae and adults of most mosquito species are not trophically specialized to any plant or animal species; therefore, the ranges of species of the family Culicidae do not directly follow those of other organisms. The distribution of some mosquito species may be limited by the presence of water bodies suitable for their larvae. NWR occupies a large territory with a total area of over 1.5 mln km^2, diverse climatic conditions, and a wide range of ecozones, from Arctic deserts to mixed forests. At the same time, in NWR there are no large arid or highland regions which could prevent the spreading of mosquitoes. Consequently, the SAT value in the collection locality appears to be an adequate climatic parameter reflecting the main features of the life cycle of mosquito species.

NWR includes some territories with relatively well-studied faunas of mosquitoes (e.g., MP, RK, SPb, and Komi) and also regions poorly studied in this respect (KP, AP, and NAO). In some cases, comparison of the northern distribution boundaries and the corresponding SAT values may be used to extrapolate the range boundary onto still unstudied territories. For example, the records of *Culiseta bergrothi* in the north of MP and the northeast of Komi (SAT 848.3°C) indicate that the species may be distributed over the largest part of NAO and AP. The records of *Culiseta morsitans* in MP and Komi

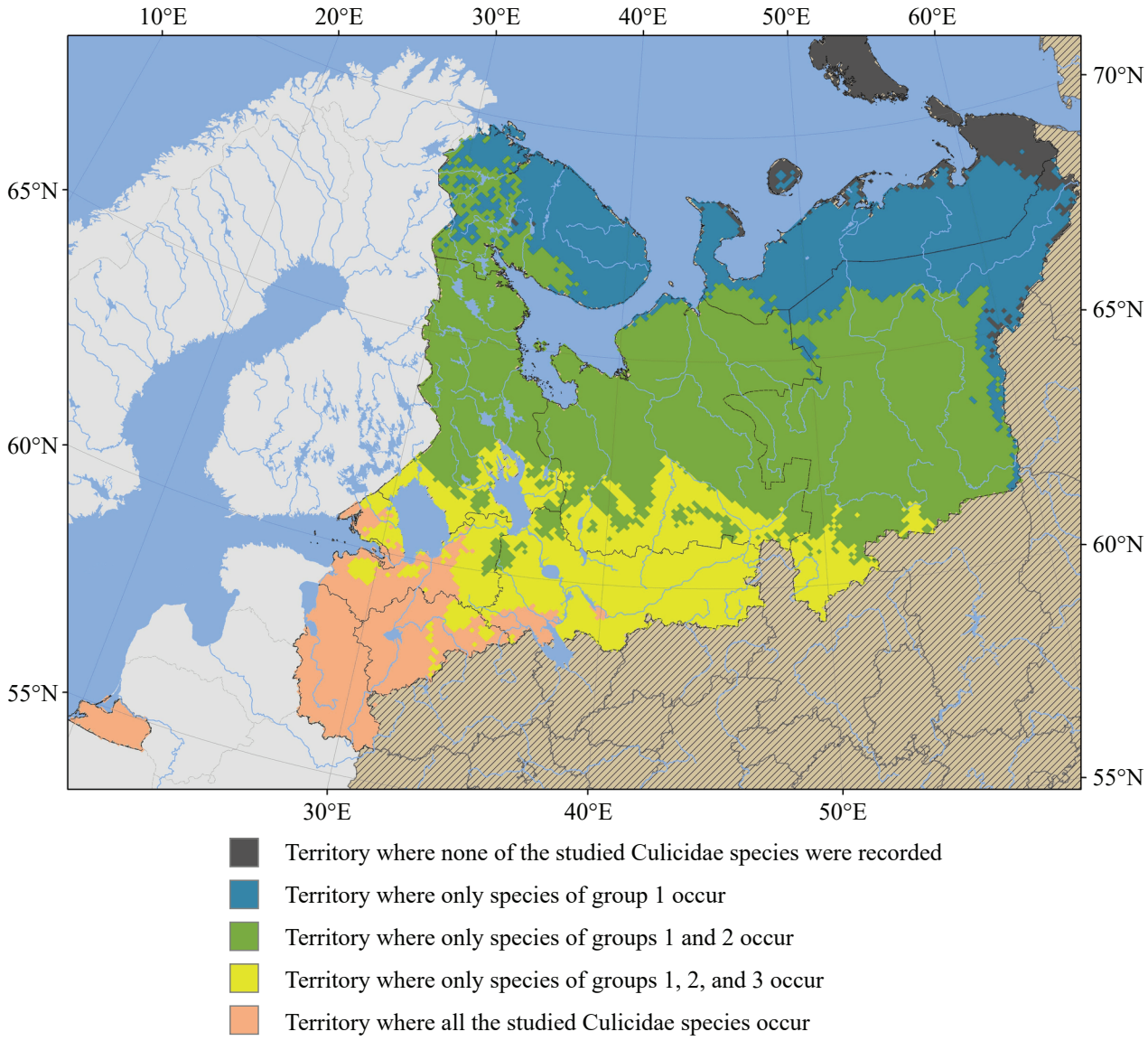

Fig. 17. Distribution of groups of Culicidae species in Northwestern Russia. The composition of groups 1–4 is explained in the text.

(SAT 1227.8°C) indicate that the species may also occur in the continental parts of AP and VP, while the records of *Coquillettidia richiardii* in RK and Komi (SAT 1966.7°C) suggest its presence in VP.

The northward expansion of a mosquito species may be limited not only by the number of days with a temperature sufficient for its preimaginal development and adult activity, but also by the low winter temperatures eliminating the insects during diapause. Most mosquitoes distributed in the high latitudes of the Holarctic (e.g., *Aedes* species) overwinter in the egg stage, but the northernmost species considered herein, *Culiseta alaskaensis* and *C. bergrothi*, diapause as adult females; yet this feature does not prevent them from spreading as far northwards as the Barents Sea coast.

CONCLUSIONS

Comparison of the species records and the SAT values for the collection localities was used to extrapolate the northern distribution boundaries of mosquito species in NWR. The northern range boundaries in different mosquito species were found to vary significantly within

the NWR territory, corresponding to the SAT values from 775.5 to 2721.8°C. For instance, the northern range boundaries of the closely related species *Culiseta alaskaensis* and *C. annulata* are located far apart: in the north of MP and Komi (SAT 775.5°C) in the former and in SPb (SAT 2226.4°C) in the latter. The mosquito species present in NWR can be included in four groups according to the common trends in their distribution. For example, the northernmost localities of mosquitoes from different genera: *Culiseta fumipennis* and *Coquillettidia richiardii*, and also *Culex territans* and *Anopheles messeae*, have nearly identical SAT values: from 1951.0 to 1966.7°C and from 1577.2 to 1587.1°C, respectively.

The results of this research may be used for species distribution modelling of such important vectors as *Anopheles maculipennis*, *A. messeae*, *Culex pipiens*, *C. modestus*, and *Coquillettidia richiardii*.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. All the applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All the procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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