Bird summer distribution patterns on islands in Onega Bay, White Sea

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Abstract

We studied avian populations and distribution patterns on 20 islands in Onega Bay, White Sea, with transect surveys completed to register selected biotic and abiotic factors in July 2020. Bird population densities proved to be the highest on small secluded islands rarely visited by humans and on treeless islands. We also found positive correlations between the species richness and the island size, presence of woody vegetation, and human visitation. It is noteworthy that although human interference can cause species diversity on the islands to increase, the relative abundance of birds declined. Furthermore, species diversity increased due to the arrival of species atypical of this region and, hence, lacking the complete set of requisite adaptations. Further human pressure on the islands can eventually destabilise their avifaunal complexes and aggravate the current transformation of northern communities in response to climate change.

Keywords: birds, White Sea, bird distribution, species composition, environmental factors

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Introduction

Islands in Onega Bay, White Sea, are crucial breeding grounds and staging areas on the Baltic-White Sea flyway for many species (Bianchi, Kokhanov and Skokova, 1975; Bianchi et al., 1993; Lehikoinen et al., 2006), including the rare, economically valuable, and those requiring protection. Moreover, many of these islands are situated within protected areas of regional and international significance (Semashko, Kolomayev and Bianchi, 1998; Semashko et al., 2000).

The history of bird studies in Onega Bay of the White Sea up to the beginning of the 21st century has been described by Bianchi (2010), Lapshin (2001, 2002), and Cherenkov, Semashko and Tertitski (2014). The studies covered by these reviews and the research by their authors were concentrated mainly in the northern part of Onega Bay, while the central and southern parts have remained understudied (Fig. 1). In the late 20th — early 21st century, surveys of the water area and individual islands in the bay by Russian ornithologists (Simonov, 2013; Cherenkov, Semashko and Tertitski, 2014; Gusev and Sokolova, 2014; Cherenkov, Tertitski and Semashko, 2015, 2016; Semashko et al., 2017a, 2017b) were complemented with several Russian-Finnish sea expeditions (Lapshin, 2001, 2002; Lehikoinen et al., 2006).

Our study continues this research (Fig. 1), intending to survey the islands, including the most difficult-to-access ones, which can only be visited on a specially arranged sea expedition in which researchers are taken to the islands by small vessels. We studied the effect of island size, location, habitat characteristics, and accessibility for humans on the distribution and abundance of birds in the summer period, corresponding to the late breeding period in a majority of local bird species (end of incubation period and feeding of nestlings, beginning of post-fledging movements).

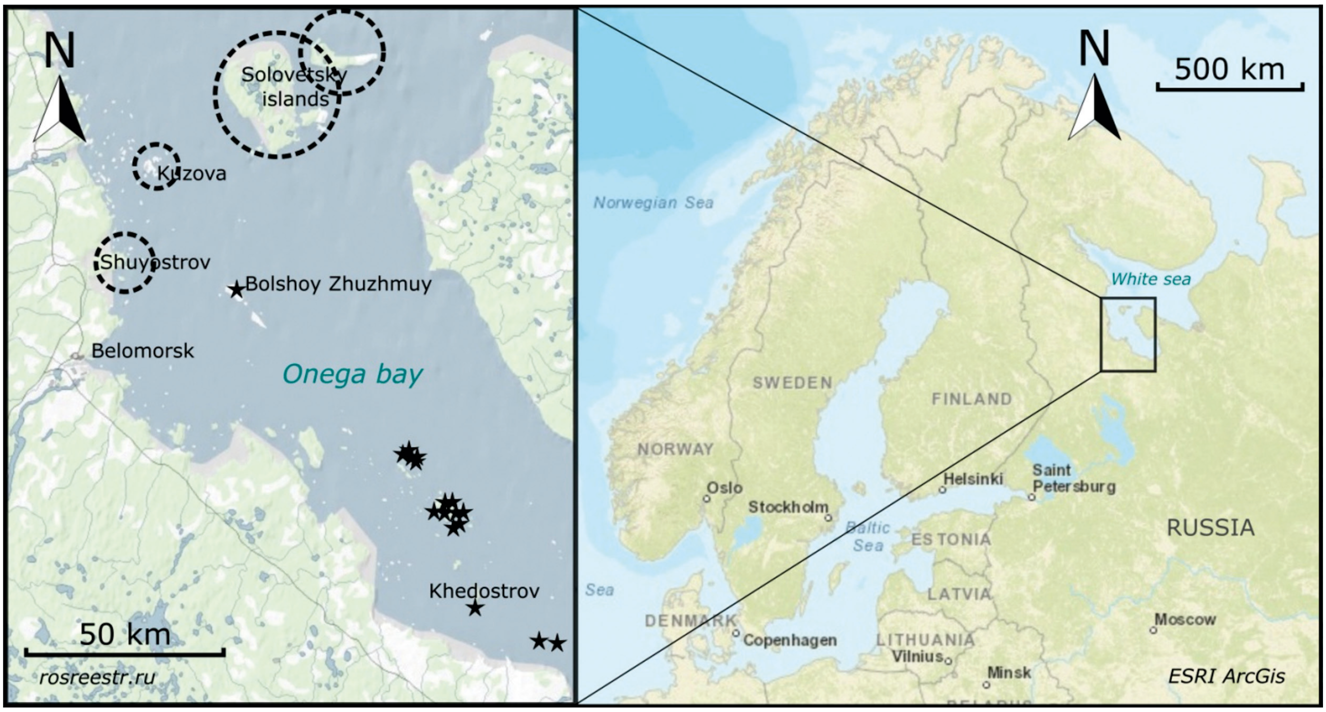


Fig. 1. Onega Bay, White Sea: circles — areas have been surveyed most thoroughly by the time of our study (see references in the text); asterisks — our surveys.

We suppose that the specifics of an island's location, its vegetation, and human visitation can significantly influence bird populations, and such knowledge can be substantial for preserving birds and their habitats. Human visitation is becoming even more relevant nowadays because people have begun visiting many islands rarely visited previously or not visited at all. Bird populations on such islands, especially on the smallest ones, can be highly vulnerable, and human presence can be critical for some of them. Therefore, it is essential to assess potential risks on time to arrange such measures as protecting the most critical breeding sites (islands with specific conditions).

Material and methods

Study area

Onega Bay is situated in the southern part of the White Sea and is its largest and shallowest bay (Fig. 1). It occupies the area between 63°50' — 65°13' N and 34°50' — 37°40' E. The bay trends northwest to southeast for some 175 km; its maximum width is 110 km, the area is approx. 12300 km^2, and the average depth is 9 m, with a maximum of 100 m (Cherenkov, Semashko and Tertitski, 2009). The bottom topography in Onega Bay is variable, especially in its western part — there are multiple elevations often reaching the surface. The bay receives discharge from many rivers, including some large ones: the Onega, Kem, and Vyg. Like the White Sea at large, the bay has semidiurnal tides, which span 1.5 in the mouth and 3 m at the top. These features entail strong currents, mixing of the entire water column, and profound warming in summer and cooling in winter. These conditions favour the development of marine communities with high biomass and productivity. Another noteworthy feature is the extensive littoral zone with fuzzy boundaries due to substantial variation in the tidal range governed by its own periodicity, wind strength and direction, and due to low-lying shore areas. Where water masses are highly dynamic, the littoral zone has a compact sandy or stony-sandy bed, while the bottom in enclosed inlets is covered in a thick blanket of silt. The littoral zone can occasionally exceed 5 km width (Cherenkov, Semashko and Tertitski, 2009).

There are more than 1000 islands in Onega Bay, most of them along the eastern shore. The largest islands lie at the Pomor Coast and in Solovetsky Archipelago. That said, islands are predominantly small, usually less than 1 ha (Fig. 1). The islands are made up of both crystalline and sedimentary rock. The climate of the Onega Bay islands, which is milder due to sea influence, features a relatively narrow annual temperature variation (21–22 °C) and some lag from the mainland in the onset of seasons. The mean annual temperature in Onega Bay ranges from +0.8 °C (Zhizhgin Island) to +1.5 °C (Onega town). Precipitation amounts are relatively low (350–400 mm), but air humidity is high, as well as the annual number of overcast days (Cherenkov, Semashko and Tertitski, 2009).

Table 1. Characteristics of transects and surveyed islands

Island	Transect, m	Area, km²	Perimeter, m	N	E
Bolshoi Zhuzhmuy*	13653	8.92	13497	64°40′	35°33′
Northern Perkhluda	6490	1.34	5805	64°20′	36°26′
Southern Perkhluda*	5378	0.85	5075	64°19′	36°28′
3rd island of Perkhluda Archipelago	619	0.04	768	64°19′	36°25′
4th island of Perkhluda Archipelago	420	0.02	623	64°18′	36°24′
Abakumikha	2792	0.41	2605	64°15′	36°35′
1st island of Ludskaya Korga	841	0.07	1265	64°14′	36°32′
2nd island of Ludskaya Korga	584	0.03	785	64°14′	36°31′
Island near Island Ugmorin	420	0.02	565	64°13′	36°33′
Ugmorin	2571	0.32	2637	64°13′	36°33′
Khlebnaya Luda	1000	0.05	885	64°13′	36°42′
Malyy Kuzmin	2194	0.21	2373	64°12′	36°43′
Island near Island Volch'ya Luda*	632	0.03	800	64°12′	36°43′
Kondostrov*	17397	12.80	24296	64°13′	36°37′
Sobachiy	792	0.04	816	64°11′	36°40′
Pnovatyy*	3091	0.32	2983	64°11′	36°39′
Island near Island Pnovatyy	370	0.02	525	64°11′	36°39′
Khedostrov	907	3.75	11448	64°02′	36°46′
Malyy Kaynets*	587	0.03	681	63°57′	37°07′
Bolshoi Kaynets	1008	0.05	817	63°56′	37°11′

The islands marked with an asterisk (*) are the most populous islands (we divided all islands into quartiles for the total number of birds that inhabit them; the most populous islands are the islands in the fourth quartile, with the highest numbers)

ANIMAL ECOLOGY

Onega Bay islands are situated in the northern taiga subzone. These islands are covered in spruce and pine north-taiga forests of various types. As a result of human activities, however, coniferous forests in disturbed areas have been replaced by coniferous/small-leaved or small-leaved stands. Meanwhile, the chilling effect of the White Sea promotes the development of plant communities resembling zonal forest-tundra and tundra communities. On many small islands and sometimes larger ones, the dominant type of forest vegetation is elfin birch woodland, which looks similar to forest-tundra birch stands. At the same time, coastal crowberry stands, which are typical of smaller islands, are similar in appearance to tundra communities. Substantial excessively wet areas on the islands are occupied by mires. Besides, the bay's mainland coast areas and the shores of many islands feature a relatively narrow strip of coastal meadows, and the northernmost areas, which are used in human activities, especially in river valleys, have man-made meadows (Cherenkov, Semashko and Tertitski, 2009).

During a 10-day bird-survey expedition in Onega Bay of the White Sea in July 2020, we visited 20 islands, including barren rocky islets (ludas): the two islands of Ludskaya Korga; Ugmorin and an islet near Island Ugmorin; Kondostrov; Abakumikha; Pnovatyy and an islet near it; Sobachiy; a nameless island near Island Volch'ya Luda; Malyy Kuzmin; Khlebnaya Luda; Bolshoi Kaynets; Malyy Kaynets; Khedostrov, four islands in the Perkhluda Archipelago; and Bolshoi Zhuzhmuy (Fig. 1).

Survey of breeding birds, broods and flocks

Preparations for field surveys using SAS. Planet (© 2007–2020, SAS. Planet Development Team) and OruxMaps Desktop 2.1.0 beta (© Jose Vazquez) included creating detailed maps of the islands to be surveyed using Yandex Satellite and Bing Satellite base maps. Navigation during transect surveys was facilitated by portable devices with Android OS and OruxMaps v.7.4.23 application for Android OS. The top view of the area to be surveyed was visualised on the device screen, indicating the observer's location and information on the scale and the transect portion covered, thus facilitating prompt and precise recording with geographic referencing. In addition, the satellite map was detailed enough to visualise solo trees, large rocks, and other landmarks.

The expedition was timed to the end of the breeding season in most resident species and the onset of post-breeding and early migrations.

The length of transects depended on the island size. Small treeless islands and luda islets were surveyed throughout. On other islands, most transects (90 %) ran along the shoreline, where broods, post-breeding congregations and migrating flocks concentrate in this period. Where shoreline length did not exceed 6 km, transects fully encircled the island. On larger islands, transects up to 17 km ran along the shoreline, preferably on different sides of the island. Some transects were made through different habitats in inner parts of larger islands, but bird numbers in those inner parts were low compared to shore areas. Each transect was surveyed once. Larger islands were visited several times, covering a new transect in a new place each time.

The length of terrestrial transects totalled 62 km (Table 1).

Surveys were done by transect count techniques with unlimited bandwidth detection (Sazonov, 1997) without scaling factors since we had exact data where both the registration and the observer's location at the time of registration were geographically referenced with high precision. This modification of the survey technique was enabled by using navigation equipment and photo recording of key encounters. While walking a transect, observers selectively photo-recorded encounters to determine bird congregations' size and species composition (using Canon EOS 1200D camera with Tamron SP 150–600 F/5 — 6.3 Di lens). Whenever possible, individual bird records were supplied with a specification of their status: breeding, in migration, in broods or flocks, etc. As a result, minimal data processing excluded any species-specific coefficients, corrections, or other manipulations, and all available data represented "raw" material.

The total number of individual bird registrations used in our study is 4105.

We cited species names and taxonomic affiliations according to the Bird Checklists of the World (Bird Checklists of the World. Europe, 2021).

Recording of biotic and abiotic factors

Bird registrations were coupled with a recording of some pre-selected parameters: the presence/absence of trees on the island, visits of birds of prey (White-tailed Eagle, Osprey), and signs of human visitation. We considered huts, remains of campfires, human paths, garbage and other things left behind by people as signs of human visitation. Such signs remained on the regularly visited islands, usually quite big islands with cloudberries situated not far from the mainland. We did not find such signs of human visitation on the small isolated islands in the most hard-to-reach places.

Further data processing using maps included determining the island area, distance to the nearest island of any area, distance to the nearest large island (conditionally not less than 3 km^2), and the shortest distance to the mainland shore. The transect length was also taken into account. All these parameters were necessary for further analysis and construction of generalized linear models that describe the distribution of birds among the islands.

During the surveys, we also hypothesised that Razorbills (*Alca torda*) choose islands with natural cavities they can use as shelter: rock crevices, spaces between large boulders, cavities between rocks and dense prostrate juniper branches. Therefore, we added cavities to the list of factors analysed (the dependent variable, in this case, was the number of Razorbill individuals).

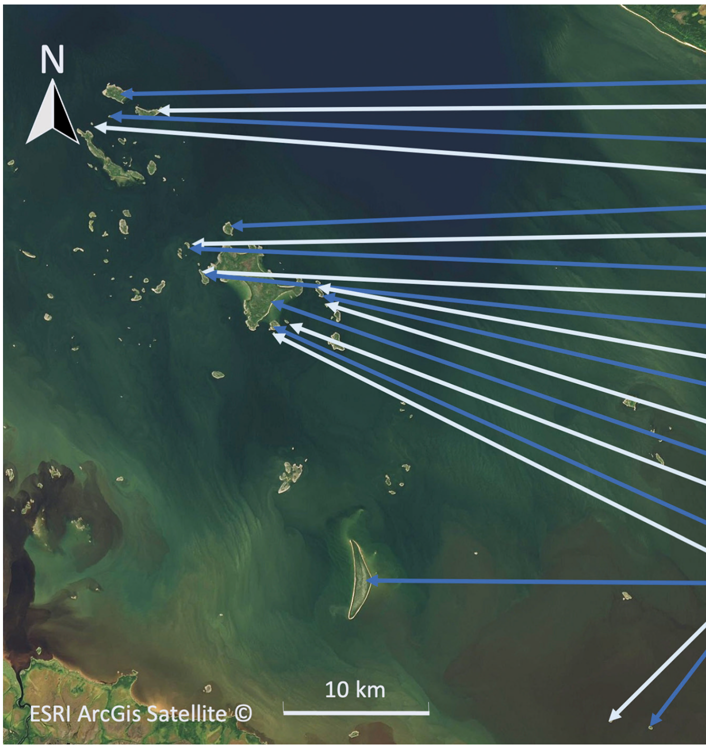
The initial plan was to include the width of the littoral zone in the analysis since this zone attracts lots of birds, especially in migration. During our surveys, however, birds did not yet congregate in the littoral zone so much, and the time of our visits to the islands did not correlate with the tidal range, so we decided to exclude the littoral zone width factor from the final analysis.

Another factor excluded from the final models was the weather, which introduced no changes to the models, since the surveys were always carried out under similar weather conditions (sunny, no rainfall, moderately windy). Owing to the overall stable weather conditions, we were able to work every day.

Statistical analyses

We selected three dependent variables for statistical processing methods: the absolute number of birds, the relative number of birds, and the number of species sighted on each island (we estimated each parameter for local breeding birds, for migrating birds, and for both local breeding and migrating birds). The parameters selected as factors (effects) were island area and perimeter, distance to the nearest island of any area, distance to the nearest large island (no less than 3 km^2), the shortest distance to the mainland shore, presence/absence of trees, presence/absence of signs of human visitation. An additional factor was the transect length.

Data distribution within groups was tested for normality by the Anderson-Darling test, package "nortest" v. 1.0–4 (Ligges and Gross, 2015). Pairwise interactions between data series were analysed by the Spearman's rank correlation method for all possible combinations of dependent variables and factors. The same method was employed to test for possible interactions between factors.



Island	Species	Number	Kurtosis
Nothern Perkhluda	*32*	*238*	*14.26*
Southern Perkhluda	*26*	*283*	*8.22*
3rd island of Perkhluda arch.	*12*	*170*	*3.40*
4th island of Perkhluda arch.	*8*	*170*	*7.21*
Abakumikha	*14*	*101*	*0.57*
1st island of Ludskaya Korga	*11*	*126*	*8.71*
2nd island of Ludskaya Korga	*11*	*79*	*4.39*
Island near island Ugmorin	*9*	*51*	*4.47*
Ugmorin	*19*	*140*	*10.34*
Khlebnaya Luda	*12*	*135*	*11.55*
Malyy Kuzmin	*15*	*91*	*2.14*
Island near island Volch'ya Luda	*5*	*350*	*4.95*
Kondostrov	*49*	*632*	*14.21*
Sobachiy	*16*	*221*	*2.01*
Pnovatyy	*15*	*283*	*3.64*
Island near island Pnovatyy	*6*	*42*	*0.11*
Khedostrov	*8*	*32*	*2.72*
Malyy Kaynets	*9*	*282*	*3.38*
Bolshoi Kaynets	*11*	*98*	*7.02*
Bolshoi Zhuzhmuy (not shown)	*35*	*581*	*18.47*

Fig. 2. Distribution of bird registrations: Species — number of species; Number — number of individuals sighted; Kurtosis — kurtosis of bird species numbers on each island.

Table 2. Numbers of Common Eider individuals along the shoreline of the surveyed islands

Island	IA	TL	ST	NB	RNB
Bolshoi Zhuzhmuy	8.92	13.65	15	202	14.8
Northern Perkhluda	1.34	6.49	49	38	5.85
Southern Perkhluda	0.85	5.38	63	35	6.51
4th island of Perkhluda arch.	0.02	0.42	100	7	16.68
Abakumikha	0.41	2.79	69	26	9.31
1st island of Ludskaya Korga	0.07	0.84	100	1	1.19
2nd island of Ludskaya Korga	0.03	0.58	100	10	17.14
Island near Island Ugmorin	0.02	0.42	100	3	7.14
Ugmorin	0.32	2.57	80	45	17.5
Kondostrov	12.8	17.40	14	145	8.33
Sobachiy	0.04	0.79	100	64	80.83
Pnovatyy	0.32	3.09	100	88	28.47
Island near Island Pnovatyy	0.02	0.37	100	6	16.23
Malyy Kaynets	0.03	0.59	100	1	1.7
Bolshoi Kaynets	0.05	1.01	100	9	8.93

Note: IA — island area, km^2; TL — transect length, km; ST — share of surveyed territory, %; NB — number of birds, ind.; RNB — relative number of birds, ind./km.

Since the presence of correlation between dependent variables and some factors reflects only particular interactions, generalized linear models, GLM, were constructed for local breeding birds using the "stats" package (package "stats" version 4.2.0, © The R Foundation) to map interactions between the studied parameters in general. All in all, we produced three models with one, two, and three fixed effects and transect length as an offset variable. The variables selected as fixed effects were island area, signs of human presence and distance to the nearest island of any area. Other factors in their various combinations failed to produce models. The optimal model was chosen using the Akaike information criterion optimized for small datasets (AICc; Burnham and Anderson, 2004). Circular bar plots with groups for bird distribution were constructed using the "tidyverse" package (Wickham et al., 2019).

Data were statistically processed in the R programming environment (R 4.0.3 x64, © R Core Team).

Results

Species composition, numbers and distribution

We detected 64 bird species during our surveys, 45 of them with signs of breeding on Onega Bay islands (Supplementary 1). The distribution of all birds (all species) among the surveyed islands is shown in Fig. 2. The higher the kurtosis in Fig. 2, the greater was the contribution of certain species to the total bird population of the island. As a rule, these would be colonial bird species. Indeed, the dominant groups of species both on all the surveyed islands in total and on the most densely populated islands were Common Eiders, Razorbills, and gulls (Figs. 3, 4). The distribution of these birds among the islands in the bay is shown in Table 2 and Figs. 5 and 6.

A remarkable finding during the expedition was breeding colonies of Razorbills (Fig. 5). Colonies on Khlebnaya Luda and a nameless islet near Volch'ya Luda amounted to some 300 adult birds. Razorbills there nested in crevices, under rocks and the shelter of dense prostrate juniper branches.

The expedition also revealed breeding colonies of gulls comprising birds of different species, including the Lesser Black-backed Gull (*Larus fuscus*) red-listed in Karelia (Artemyev et al., 2020). The largest colonies (Mew Gull (*Larus canus*), Herring Gull (*Larus argentatus*), Lesser Black-backed Gull (*Larus fuscus*), Great Black-backed Gull (*Larus marinus*) were spotted on the relatively large islands Bolshoi Zhuzhmuy and Kondostrov, on an islet near the island Northern Perkhluda, and on the islands Pnovatyy and Malyy Kaynets (Fig. 5).

An occupied White-tailed Eagle (*Haliaeetus albicilla*) nest was found on the island Northern Perkhluda. Khedostrov Island also had signs of breeding of this species. Signs of having been visited by White-tailed Eagles (White-tailed Eagle feathers, remains of its prey birds) were found on almost all islands, but more abundantly on larger islands, on islands situated close to neighbouring islands, and on islands lying near to the ones where White-tailed Eagles bred.

Our expedition also made several relatively unusual registrations: Blyth's Reed Warbler (*Acrocephalus dumetorum*) broods with young fledglings fed by the parents were encountered on Kondostrov and Northern

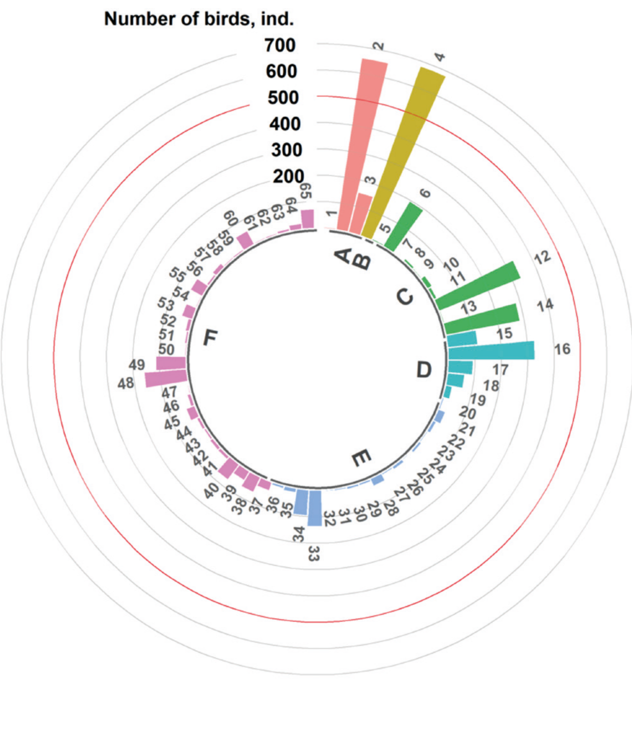


Fig. 3. Contributions of different species to the total number of birds recorded from all the surveyed islands. A — Auks, B — Eiders, C — Waders, D — Gulls, E — Other non-passerines, F — Passerines, 1 — *Alle alle*, 2 — *Alca torda*, 3 — *Cepphus grylle*, 4 — *Somateria mollissima*, 5 — *Scolopax rusticola*, 6 — *Haematopus ostralegus*, 7 — *Hydrocoloeus minutus*, 8 — *Arenaria interpres*, 9 — *Tringa ochropus*, 10 — *Tringa nebularia*, 11 — *Actitis hypoleucos*, 12 — *Calidris alpina*, 13 — *Numenius arquata*, 14 — *Numenius phaeopus*, 15 — *Larus argentatus*, 16 — *Larus canus*, 17 — *Larus fuscus*, 18 — *Sterna paradisaea*, 19 — *Larus marinus*, 20 — *Anas crecca*, 21 — *Bucephala clangula*, 22 — *Lyrurus tetrix* , 23 — *Mergus merganser*, 24 — *Bonasa bonasia*, 25 — *Tetrao urogallus*, 26 — *Gavia arctica*, 27 — *Grus grus*, 28 — *Stercorarius parasiticus*, 29 — *Lagopus lagopus*, 30 — *Haliaeetus albicilla*, 31 — *Cygnus olor*, 32 — *Pandion haliaetus*, 33 — *Phalacrocorax carbo*, 34 — *Mergus serrator*, 35 — *Dendrocopos major*, 36 — *Falco subbuteo*, 37 — *Fringilla coelebs*, 38 — *Parus major*, 39 — *Corvus cornix*, 40 — *Oenanthe oenanthe*, 41 — *Erithacus rubecula*, 42 — *Loxia pytyopsittacus*, 43 — *Regulus regulus*, 44 — *Muscicapa striata*, 45 — *Spinus spinus*, 46 — *Corvus corax*, 47 — *Phylloscopus trochiloides*, 48 — *Motacilla alba*, 49 — *Poecile montanus*, 50 — *Tarsiger cyanurus*, 51 — *Emberiza citrinella*, 52 — 25 *Turdus philomelos*, 53 — *Turdus pilaris*, 54 — *Turdus merula*, 55 — *Phoenicurus phoenicurus*, 56 — *Pyrrhula pyrrhula*, 57 — *Acrocephalus dumetorum*, 58 — *Sylvia curruca*, 59 — *Anthus trivialis*, 60 — *Anthus pratensis*, 61 — *Bombycilla garrulus*, 62 — *Troglodytes troglodytes*, 63 — *Acanthis flammea*, 64 — *Loxia curvirostra*, 65 — *Phylloscopus trochilus.*

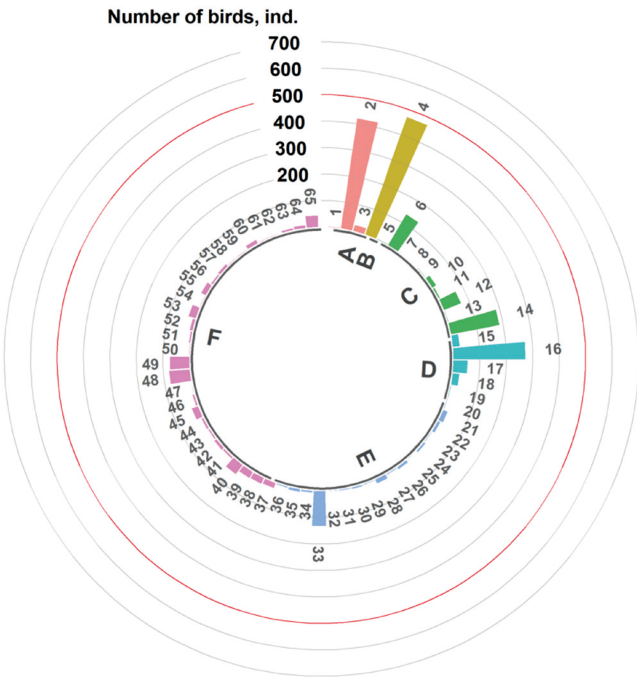


Fig. 4. Contributions of different species to the total number of birds recorded from the most 33 populous islands (marked with an asterisk (*) in Table 1). A — Auks, B — Eiders, C — Waders, D — Gulls, E — Other non-passerines, F — Passerines, 1 — *Alle alle*, 2 — *Alca torda*, 3 — *Cepphus grylle*, 4 — *Somateria mollissima*, 5 — *Scolopax rusticola*, 6 — *Haematopus ostralegus*, 7 — *Hydrocoloeus minutus*, 8 — *Arenaria interpres*, 9 — *Tringa ochropus*, 10 — *Tringa nebularia*, 11 — *Actitis hypoleucos*, 12 — *Calidris alpina*, 13 — *Numenius arquata*, 14 — *Numenius phaeopus*, 15 — *Larus argentatus*, 16 — *Larus canus*, 17 — *Larus fuscus*, 18 — *Sterna paradisaea*, 19 — *Larus marinus*, 20 — *Anas crecca*, 21 — *Bucephala clangula*, 22 — *Lyrurus tetrix* , 23 — *Mergus merganser*, 24 — *Bonasa bonasia*, 25 — *Tetrao urogallus*, 26 — *Gavia arctica*, 27 — *Grus grus*, 28 — *Stercorarius parasiticus*, 29 — *Lagopus lagopus*, 30 — *Haliaeetus albicilla*, 31 — *Cygnus olor*, 32 — *Pandion haliaetus*, 33 — *Phalacrocorax carbo*, 34 — *Mergus serrator*, 35 — *Dendrocopos major*, 36 — *Falco subbuteo*, 37 — *Fringilla coelebs*, 38 — *Parus major*, 39 — *Corvus cornix*, 40 — *Oenanthe oenanthe*, 41 — *Erithacus rubecula*, 42 — *Loxia pytyopsittacus*, 43 — *Regulus regulus*, 44 — *Muscicapa striata*, 45 — *Spinus spinus*, 46 — *Corvus corax*, 47 — *Phylloscopus trochiloides*, 48 — *Motacilla alba*, 49 — *Poecile montanus*, 50 — *Tarsiger cyanurus*, 51 — *Emberiza* 46 *citrinella*, 52 — *Turdus philomelos*, 53 — *Turdus pilaris*, 54 — *Turdus merula*, 55 — *Phoenicurus phoenicurus*, 56 — *Pyrrhula pyrrhula*, 57 — *Acrocephalus dumetorum*, 58 — *Sylvia curruca*, 59 — *Anthus trivialis*, 60 — *Anthus pratensis*, 61 — *Bombycilla garrulus*, 62 — *Troglodytes troglodytes*, 63 — *Acanthis flammea*, 64 — *Loxia curvirostra*, 65 — *Phylloscopus trochilus.*

Perkhluda; a singing and anxious male Greenish Warbler (*Phylloscopus trochiloides*) was sighted on Kondostrov; two Mute Swan (*Cygnus olor*) individuals were seen on the water near Kondostrov; one Little Auk (*Alle alle*) was noted near Kondostrov (see below).

Factors influencing the distribution of birds among islands and their numbers

Only a half of the selected factors that characterise the islands produced reliable effects on birds' numbers and species composition (Table 3). It should be kept in mind that factors such as island perimeter and transect length (mainly running along the shoreline) were predictably intercorrelated ($S_{19,19}$ = 104, *rho* = 0.9218, $p < 0.0001$; island perimeter and area, $S_{19,19}$ = 24, *rho* = 0.9820, $p < 0.0001$). The rest of the factors showed no pairwise correlations.

Among the generalized linear models made for relative numbers of local breeding birds and various combinations of fixed effects, the value of the Akaike information criterion (AIC) was the lowest in the model incorporating island area, distance to the nearest island (of any area) and signs of human presence as the fixed component set and transect length as an offset variable (Table 4).

Discussion

Species composition, numbers and distribution

The species composition of birds observed during the expedition (Supplementary 1) generally agrees with previous reports by other researchers from this region (Lapshin, 2001, 2002; Lehikoinen et al., 2006; Bianchi, 2010; Simonov, 2013; Cherenkov, Semashko and Tertitski, 2014; Gusev and Sokolova, 2014; Cherenkov, Tertitski and Semashko, 2015, 2016; Semashko et al., 2017a, 2017b). That said, the birds in our counts were chiefly those breeding directly on the surveyed islands (their breeding population), and less so — birds starting migration via these islands.

Common Eider (Figs. 3, 4; Table 2) and Razorbill (Fig. 3) were the most abundant species, which formed large colonies. The second most abundant group was Mew Gulls — the dominant gull species (Figs. 3, 5), who also formed dense breeding colonies, as well as Dunlin (*Calidris alpina*) and Whimbrel (*Numenius phaeopus*) — waders whose migration via the islands already started, and who had formed congregations for migration (Fig. 3). A critical remark is that many birds of passage whose migration had not yet started and some rare and scarce species were not covered by the surveys.

Our studies have produced new data on the summer distribution of breeding birds among islands in the bay (Tables 2, 3; Figs. 2, 4, 5), which is particularly important when speaking of the Common Eider (Table 3) — a species of economic significance, which requires especially thoughtful protection regulations (Goryashko, 2020). Onega Bay of the White Sea is where most Common Eiders of the Republic of Karelia breed (Matantseva and Simonov, 2020).

An interesting discovery was the finding of several breeding colonies of Razorbills (Fig. 3). In addition, valuable data were also obtained regarding the White-tailed Eagle — another species red-listed in the Republic of Karelia (Artemiev et al., 2020) (see below).

Table 3. Factors that reliably influence birds' numbers and species composition on the surveyed islands

Avifauna parameters	Island parameters	*S*	*p*	*rho*
Relative number (all), ind./km	Transect length, km	2287.4	0.0003	–0.7199
Relative number (local), ind./km	Transect length, km	2244.3	0.0008	–0.6875
Relative number (migrants), ind./km	Transect length, km	2191.3	0.0020	–0.6476
Relative number (all), ind./km	Island area, km^2	2407.6	< 0.0001	–0.8102
Relative number (local), ind./km	Island area, km^2	2368	0.0001	–0.7805
Relative number (migrants), ind./km	Island area, km^2	2264	0.0008	–0.7023
Relative number (all), ind./km	Distance to the nearest large island, km	569.71	0.0084	0.5716
Relative number (local), ind./km	Distance to the nearest large island, km	569.71	0.0084	0.5716
Relative number (migrants), ind./km	Distance to the nearest large island, km	552.83	0.0068	0.5843
Relative number (all), ind./km	Presence of trees	2339.9	0.0001	–0.7593
Relative number (local), ind./km	Presence of trees	2268.8	0.0005	–0.7059
Relative number (migrants), ind./km	Presence of trees	2292.0	0.0003	–0.7233
Relative number (all), ind./km	Human visitation	2196.9	0.0018	–0.6518
Relative number (local), ind./km	Human visitation	2142.3	0.0042	–0.6108
Relative number (migrants), ind./km	Human visitation	2035.8	0.0161	–0.5307
Number of individuals	Transect length, km	650.49	0.0213	0.5109
Number of species (all)	Transect length, km	210.63	0.0001	0.8416
Number of species (local)	Transect length, km	151.95	< 0.0001	0.8858
Number of species (migrants)	Transect length, km	684.23	0.0300	0.4856
Number of species (all)	Island area, km^2	331.99	< 0.0001	0.7504
Number of species (local)	Island area, km^2	233.11	< 0.0001	0.8247
Number of species (all)	Presence of trees	504.58	0.0035	0.6206
Number of species (local)	Presence of trees	458.40	0.0017	0.6553
Number of species (all)	Human visitation	662.16	0.0241	0.5021
Number of species (local)	Human visitation	595.65	0.0116	0.5521
Number of Razorbill, ind.	Presence of cavities*	301.86	0.0001	0.7730
Number of Common Eiders, ind.	Island area, km^2	696.98	0.0339	0.4760

Spearman's rank correlation coefficient, α = 5 % (all) — a parameter for all birds (local breeding and migrating birds); (local) — a parameter for local breeding birds only; (migrants) — a parameter for migrating birds only. The line marked with an asterisk (*) means the presence of natural cavities that can be used as a shelter: rock crevices, spaces between large boulders, cavities between rocks and prostrate juniper thickets.

Table 4. Characteristics of the generalized linear models that describe variations in relative numbers of local breeding birds per kilometer of a transect on the surveyed 20 islands in Onega Bay, White Sea

Variable	B ± SE	*t*	*p*
(Intercept)	–2.283e+02 ± 1.114e+02	–2.048	0.063
Island area	–8.456e–03 ± 8.884e–04	–9.518	< 0.001
Human presence	–6.666e+03 ± 2.671e+02	–24.957	< 0.001
Island area and human presence	7.676e–03 ± 8.889e–04	8.635	< 0.001
Distance to the nearest island, and human presence	3.496 ± 0.262	13.308	< 0.001
Island area, distance to the nearest island, and human presence*	–5.005e–06 ± 2.197e–06	–2.278	0.0418

The model marked with an asterisk (*) has the lowest values of the Akaike information criterion (AIC).

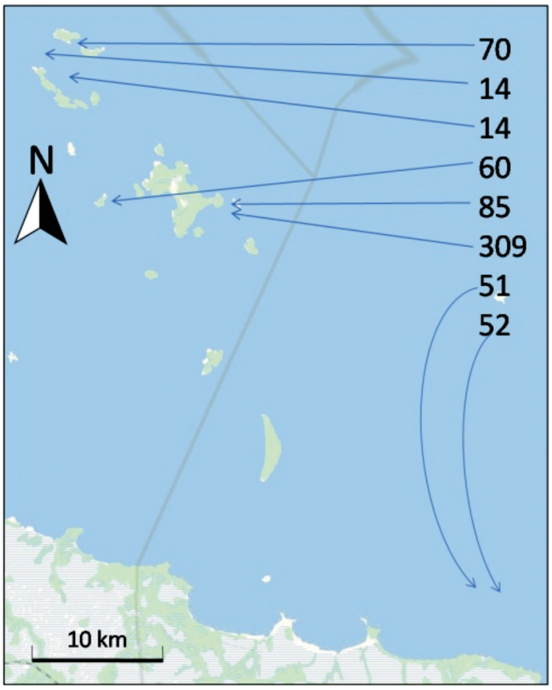


Fig. 5. Number of birds in Razorbill colonies on the surveyed islands.

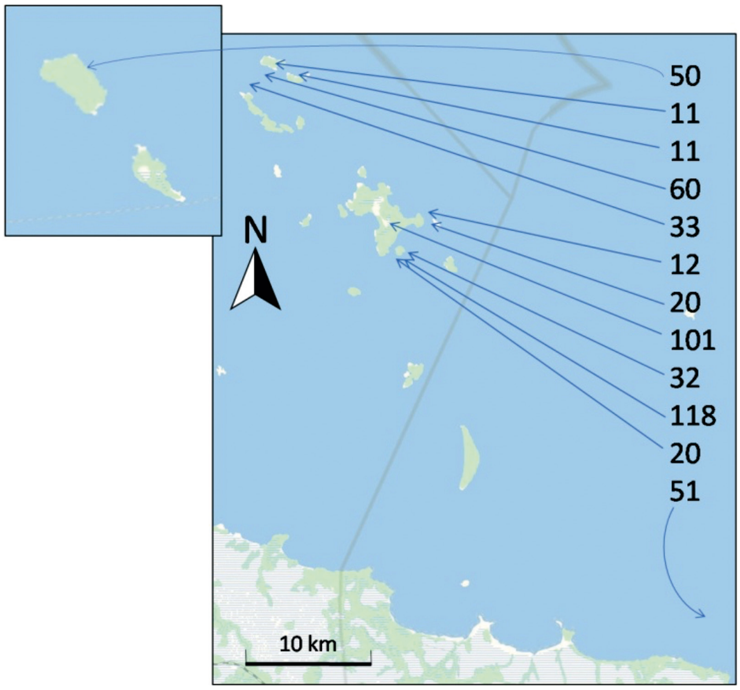


Fig. 6. Gull congregations on the surveyed islands, ind.

Also, two Mute Swans were encountered during the expedition. The White Sea region is outside of the species' breeding range, but the birds are occasionally spotted in the area in summer, especially in the past few decades (Lehikoinen et al., 2006; Cherenkov, Semashko and Tertitski, 2014). It is yet unclear why they come to the area. Supposedly, Mute Swan sightings in the north of European Russia have become more frequent as the species' West European population has increased and its breeding range has expanded (Cherenkov, Semashko and Tertitski, 2014).

Another rather uncommon registration is that of a Little Auk near Kondostrov. Little Auks breed much farther north; their breeding grounds in Russia are on Novaya Zemlya and Franz Josef Land. In summer, solo individuals with no evidence of breeding are sometimes sighted near the shore at the northern tip of the Kola Peninsula. Nomadic birds can reach as far as the White Sea mouth (Gavrilo, 2020). Our registration should probably be regarded as a vagrant.

Special attention should be given to facts of confirmed breeding of Blyth's Reed Warbler (broods with younger fledglings were observed) and registrations of a singing and anxious male Greenish Warbler. Both species are at the margin of their distribution, and our registrations corroborate the postulates that the distribution of Blyth's Reed Warbler and Greenish Warbler has been expanding northwestwards (Cherenkov, Semashko and Tertitski, 2014; Kalyakin and Voltzit, 2020; Noskov et al., 2020).

Factors influencing the distribution of birds among islands and their numbers

We investigated chosen biotic and abiotic factors potentially influencing the distribution of birds among the islands, including their numbers and species diversity (Tables 3, 4). Besides that, we checked for a possible correlation of bird numbers and species diversity with transect length (Table 3), since the length of transects in our study varied substantially (Table 1), potentially affecting the resulting data. The direct relationship between the number of birds and species (of all categories) sighted and the transect length (Table 3) is self-explanatory (as a rule, an observer can see more birds of different species on the longer routes, which is especially important for large islands). On the other hand, the inverse relationship between the relative bird number and transect length (Table 3) occurred because bird colonies were often concentrated on small islets (Figs. 5, 6), where the islet size limited the transect length (a loop along the shoreline).

As a result, the study demonstrated that the relative numbers (per kilometre of transect/shoreline) of birds (separately local breeding and migrating and all species together) on the surveyed islands negatively correlated with the island area, presence of trees, and human visitation and positively correlated with the distance to the nearest large island (Table 3). Overall, a conclusion from the patterns revealed (Table 3) and the outputs of the generalized linear models (Table 4) characterising the combined effect of the analysed factors on relative species numbers is that birds form the highest densities on smaller secluded islands devoid of woody vegetation. The main reason for these correlations is that such islands were often harbouring colonies of Razorbills and gulls (Figs. 5, 6), which contribute substantially to total bird numbers (Fig. 3). Furthermore, birds of other species also tended to prefer such islands, forming the densest breeding colonies and congregations of broods and flocks. In particular, migrating flocks of Dunlins stayed on the shores of such islands, and Common Eiders congregated in adjacent water areas (Table 2).

Isolated islands (situated far away from the mainland and other islands) are the most difficult to reach for people (and their accompanying dogs), and for large terrestrial carnivores, which can potentially swim to an island near the mainland and, via it, move farther into the bay over a chain of closely spaced islands, crossing the distances between them by swimming. Moreover, some predator species, such as foxes, may have settled from the mainland to the faraway islands using such chains of islands according to the concept of stepping stone islands (Gilpin, 1980). As a result, terrestrial birds inhabiting islands near the mainland or connecting it with other islands' chains suffer from the threat of such predators. At the same time, birds on islands located far from mainland shore and other islands are safe in this regard, which undoubtedly makes such islands more attractive.

Additionally, White-tailed Eagle visits also occur more frequently on larger islands and nearby archipelagoes than on small secluded islets. Therefore, it is reasonable to assume that birds of prey also rarely fly to the most remote islets if there are island clusters they can examine much more efficiently.

Meanwhile, not all islands with the said properties (isolated relatively small islands without woody vegetation and no human visitation signs) had Razorbill colonies. Among all the analyzed factors, we found a direct correlation only between the number of Razorbills and the presence of natural cavities they can use as shelter: rock crevices, spaces between large boulders, cavities between rocks and dense prostrate juniper branches (Table 3).

In turn, the number of local breeding species recorded on an island positively correlated with its size and the presence of woody vegetation (Table 3). The associations are predictable and in good agreement with island zoogeography concepts, as the number of habitats usually positively correlates with the number of species, and bigger islands usually have more extensive species diversity (MacArthur and Wilson, 1967; Guo, 2014; Valente et al., 2020). Indeed, the species diversity is composed of seabirds and shorebirds on almost all the surveyed islands and enriched with forest species on forested islands. The same correlation was found for the number of all species (local breeding and migrating), but we consider that because of local birds' predominant impact.

According to the classical concepts of island biogeography, species richness decreases on islands situated farther away from the source of settlement, a mainland or a big island (Valente et al., 2020). However, we have not found such a relationship. Clearly, for such mobile animals as birds, the distances between islands in the relatively narrow Onega Bay are not significant. Moreover, even on a larger scale, birds are less affected by the island's isolation (Guo, 2014).

Besides, the number of local breeding species on an island positively correlated with human visitation (Table 3). As a rule, islands with regular human presence had habitats altered by human activity — some of them had natural coniferous forest replaced with small-leaved forest patches, some areas were cleared of forest for human needs, such as grasslands or even kitchen plots. These disturbed habitats attract birds typical of southerner regions, such as Blyth's Reed Warbler and Greenish Warbler. Overall, species diversity is greater on islands with a higher diversity of habitats (including forest and man-made habitats), which contributes to the correlations of the number of species with the island size, and as we have said above, corresponds to island zoography concepts (MacArthur and Wilson, 1967; Guo, 2014; Valente et al., 2020).

Meanwhile, it is noteworthy that although human presence causes some increase in the bird species diversity on the islands, the relative abundance of species declines (Table 3). Furthermore, the species diversity increases due to the arrival of species atypical of this region and, hence, lacking the full set of requisite adaptations. A number of studies have demonstrated that in many northern regions, the share of southern species is increasing, and the share of northern species is declining as the northern limits of the range, and population densities are shifting southwards, especially in southern species (Brommer, Lehikoinen and Valkama, 2012; Lindström et al., 2013; Virkkala and Lehikoinen, 2014, 2017; Lehikoinen and Virkkala, 2016; Fraixedas et al., 2017; Virkkala et al., 2018). Northwest Russia is also experiencing an ongoing species turnover. Researchers working here also express concerns that the decline in the share of northern species in local communities and their replacement with southern species not adapted to living in the north (first of all to the short time interval suitable for breeding and moult) can shatter the stability of these communities (Sazonov et al., 2002; Khokhlova and Artemiev, 2007; Danilov, 2010; Khokhlova and Artemiev, 2011; Simonov and Matantseva, 2020).

Such instability of populations may be further compounded by the island effect (MacArthur and Wilson, 1967). Generally, island communities are much more straightforward by species, spatial and functional structure than continental ones. However, simple structure and poor species composition are known to be highly unstable and weak buffering. Thus, island populations are highly vulnerable to possible impacts (Levins, 1969; Hanski and Gilpin, 1991). In this sense, the concepts of island biogeography overlap with those of metapopulation theory (Levins, 1969). Neighbouring islands' populations can be considered meta-populations, and the congregations of islands can be considered fragmented landscapes. Potential population growth is limited in a fragmented landscape, which can be further exacerbated in a dynamically fragmented landscape (Hanski, 1999), i.e., any changes, including those provoked by humans. Therefore, further human pressure on the islands can eventually destabilise their avifaunal complexes and aggravate the effect of the current transformation of northern communities in response to climate change.

Conclusions

The expedition produced data on the species composition and numbers of birds on islands in Onega Bay of the White Sea. We detected several breeding colonies of Razorbill and various gull species, described congregations of Common Eider, observed birds of early migrating species, gathered data on some red-listed species and species whose distributions have expanded northwestwards.

Bird population densities proved to be the highest on small secluded islands rarely visited by humans and treeless islands. The high bird population densities on such islands (and surrounding waters) were mainly generated by abundant species such as the Common Eider, Razorbill, and gulls. We also found positive correlations between species richness and the island size, presence of woody vegetation, and human visitation.

In turn, the number of species positively correlated with the island size, presence of woody vegetation, and human visitation (and anthropogenetic habitats). All these factors reflect a variety of habitats. That is why these associations are in good agreement with the zoogeography concepts, as the number of habitats usually positively correlates with the number of species (MacArthur and Wilson, 1967; Valente et al., 2020).

It is noteworthy that although human interference can cause the bird species diversity on the islands to increase, the relative abundance of the species declines. Furthermore, species diversity increases due to the arrival of species atypical of this region and, hence, lacking the complete set of requisite adaptations. Thus, further human pressure on the islands can eventually destabilise their avifaunal complexes and aggravate the effect of the current transformation of northern communities in response to climate change.

The findings of this study can serve as the ground for establishing a stricter protection status for islands in Onega Bay of the White Sea, first of all for small isolated islets situated far away from both the mainland shore and larger islands regularly visited by humans.

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