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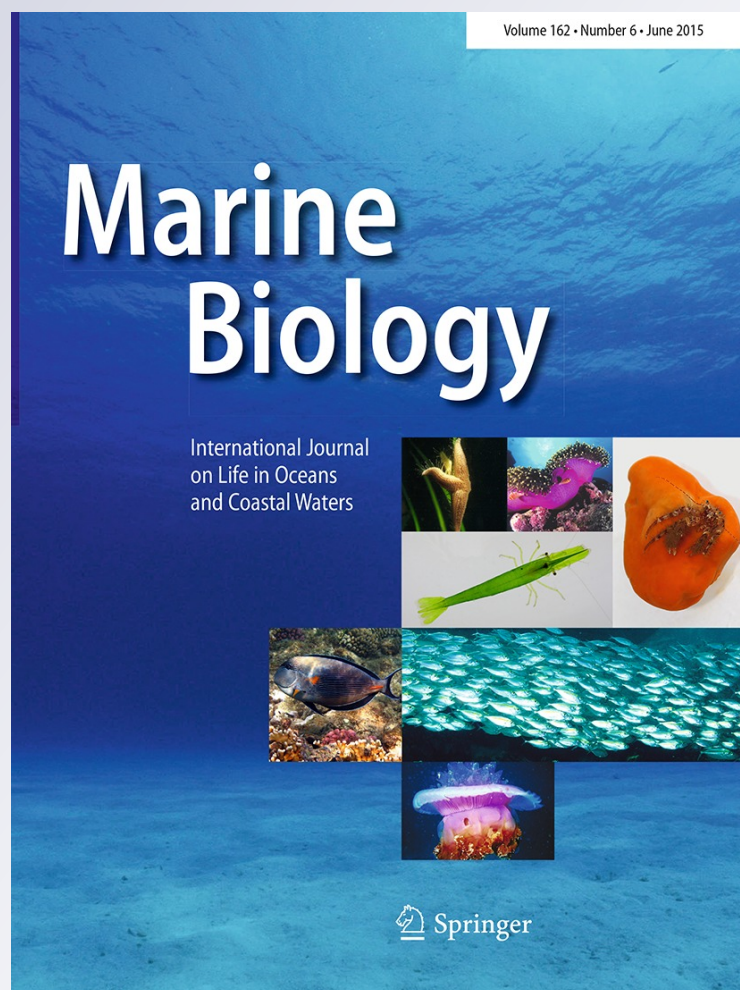
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The Crested Auklet, *Aethia cristatella* (Alcidae, Charadriiformes), does not vary geographically in genetics, morphology or vocalizations

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Abstract The study of population differentiation is essential for understanding species evolution and ecology. Despite a large amount of published works in this area of study, the prediction of population structure in a number of animal species and, particularly, in seabirds remains difficult. The Crested Auklet (*Aethia cristatella*) is a small, planktivorous seabird species that breeds in colonies on islands and along the coastline of the North Pacific. Despite their vast breeding area and huge population numbers, the phenotypic features of adult birds from different colonies and genetic population variability have not been studied yet. Here we conducted a combined study of population differentiation in the Crested Auklet, using both phenotypic and genetic features. Data were collected at nine points across the species' distribution range from 1988 to 2012. We analyzed population variability of the mitochondrial control region fragment, microsatellites, two types of vocalizations (barks and trumpet calls), morphometric and ornamentation measurements. However, we did not detect

any obvious cues to different populations, either in genetic, morphometric or acoustic variables. Crested Auklets from different geographic areas do not express any genetic differences. We surmise that the absence of population separation in Crested Auklet can be explained by an important ecological characteristic of the species: these birds are pelagic during non-breeding season; therefore, young birds likely migrate far away from their natal colonies during their first year of life and do not often return to breed at their native colony.

Introduction

Knowledge of population differentiation is essential for understanding many aspects of species' evolution and ecology, such as migratory routes, dispersal of young and process of speciation. Within broad groups, like vertebrates or invertebrates, the extent of genetic structure is often inversely related to dispersal capability (Bohonak 1999). It is more difficult to relate differentiation to life-history traits at levels such as species, or ecological groupings like seabirds (Dearborn et al. 2003; Friesen et al. 2007; Burney and Brumfield 2009). Wing morphology, capture–recapture and satellite telemetry data indicate that many seabird species travel hundreds and thousands of miles during foraging or migration and therefore have the potential to disperse and breed far from their natal colonies (Pennycuik 1982; Dearborn et al. 2003; Meyers and Stakebake 2005; Steeves et al. 2005; Friesen et al. 2007). Accordingly, little population differentiation is expressed genetically in some seabird species (Moum et al. 1991; Burg and Croxall 2001; Moum and Arnason 2001; Pearce et al. 2002; Genovart et al. 2003). In contrast, strong genetic population structure and even cryptic species have been found in other studies,

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e.g., on Procellariiformes (Burg and Croxall 2001; Friesen et al. 2006; Smith and Friesen 2007; Smith et al. 2007) and Alcidae (Birt-Friesen et al. 1992; Friesen et al. 1996a, b, 2005; Ibaruchi et al. 2011). We analyzed genetic population structure in a previously unstudied alcid species, and we compared patterns of differentiation across genetic, phenotypic and vocal traits because there are examples of discordant patterns in other species (Louis and Barlow 1987; Soha et al. 2004; Wright et al. 2005).

We studied Crested Auklet (*Aethia cristatella*), a small, planktivorous seabird that breeds in colonies of up to a million birds on islands and along coastlines of the North Pacific (Fig. 1). The species' winter range is poorly documented. It is known that birds winter in ice-free waters in the southern portion of their breeding range, migrating as far as northern Japan (Shuntov 1965; Jones 1993a; Gaston and Jones 1998). Crested Auklets are highly social and have a rich repertoire of visual and vocal displays (Jones 1993a; Gaston and Jones 1998). The species is socially monogamous, and both parents share incubation and chick rearing (Jones 1993a). However, about 10 % of copulations occur between unpaired birds, and up to 54 % pairs divorce between breeding seasons (Jones and Hunter 1999; Fraser et al. 2004). Despite the high divorce rate, adults express high nest-area fidelity from year to year (Zubakin 1990; Jones and Hunter 1999; Fraser et al. 2004; Jones et al. 2004; Klenova et al. 2012a). Natal-site fidelity is an

important component of population differentiation but has not been studied in this species (Jones 1993a; Nettle-ship 1996; Gaston and Jones 1998). Genetic population structure was poorly studied in the Crested Auklet. Walsh et al. (2005) found only weak evidence of genetic differentiation in α -enolase intron VIII and cytochrome *b* fragment in a small sample of Crested Auklets (81 birds from 12 localities). No subspecies of the species have been proposed using traditional characters of study skins (measurements; plumage), and phenotypic geographic variation has not been studied. However, adults from Buldir Island and Saint Lawrence Island colonies differ slightly in body size and plumage ornamentation (Jones 1993a; Gaston and Jones 1998). Vocalizations of breeding adults have been described from colonies in the Bering Sea and Sea of Okhotsk but also have not been analyzed for geographic variation (Buldir Island—Seneviratne et al. 2009; Talan Island—Zubakin et al. 2010; Klenova et al. 2011, 2012a, b). Here we studied geographic variation in morphometrics, vocalization and genetics based on samples from nine breeding colonies. Taking into account the high level of nest-site fidelity, the presence of two separate main winter regions in Crested Auklet (Gaston and Jones 1998) and the well-documented phenotypic variability in the closely related Whiskered Auklet (*Aethia pygmaea*; Feinstein 1959; Klenova et al. 2013), we predicted to find population structure in the Crested Auklet.

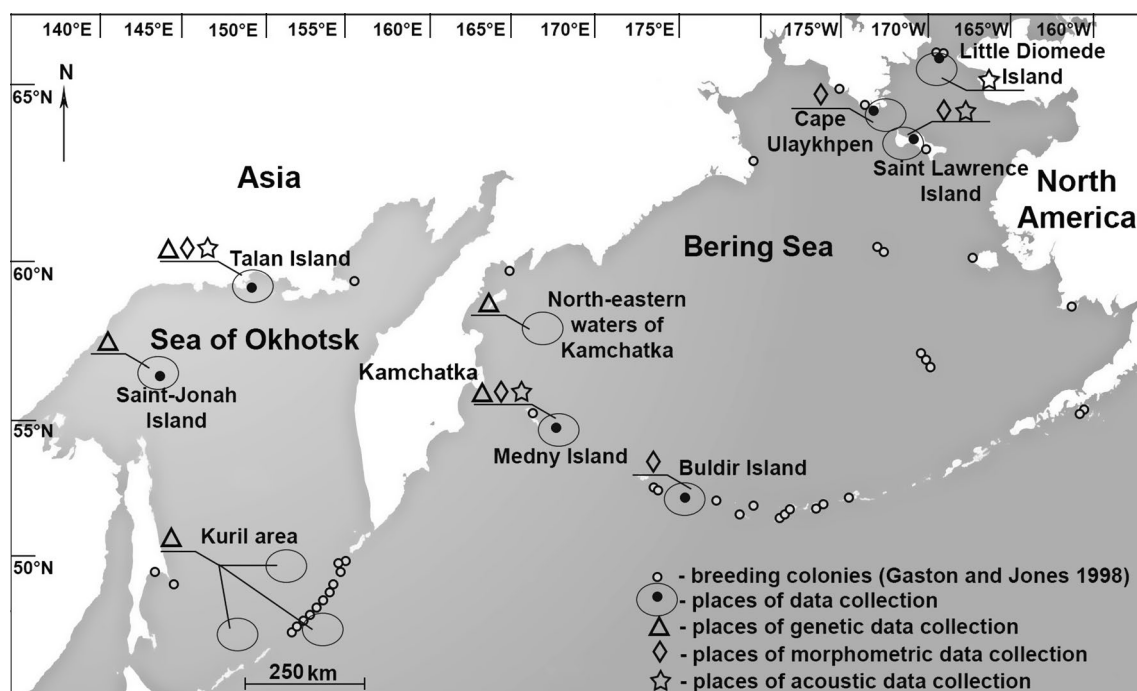


Fig. 1 Main breeding colonies of the Crested Auklet and places of data collection (© Google, INEGI 2015)

Materials and methods

Study site

Data were collected from 1988 to 2012 at nine colonies, located on the islands of Talan, Saint-Jonah (Iona), Medny, Buldir, Little Diomede and Saint Lawrence, and in the area of the Kuril Islands (hereafter “Kuril area”), the north-eastern waters of the Kamchatka Peninsula (“Kamchatka” hereafter) and Cape Ulaykhpen. Details of the samples (years, sample sizes and types) and site (geographic coordinates) are summarized in Fig. 1 and Table 1.

The seabird colonies at Talan, Saint-Jonah, Buldir, Little Diomede and St. Lawrence islands, and at Cape Ulaykhpen are among the largest in the North Pacific. Island areas are ~2.5, 0.2, 19.3, 7.3 and 4640 km², respectively; corresponding estimates of the number of Crested Auklets are ~260,000–300,000; 9,000; 280,000; 100,000; 517,000; and 90,000 (Gaston and Jones 1998; Denlinger 2006; Gibson and Byrd 2007; Andreev et al. 2010, 2012; N.B. Konyukhov pers comm). Medny is a large island (186 km² in area) with a large (>500,000 birds) seabird colony, but only ~100 Crested Auklets are present (Artukhin 1999; Klenova and Shienok 2012).

Our samples of birds from the Kuril area and Kamchatka were bycatch in salmon gillnets in the open sea (Artukhin et al. 2010). Near the Kurils, birds were caught near large colonies during the breeding season, so we assume that these individuals bred there. However, our Kamchatka sample was taken far from main colonies at the end of May and beginning of June (Fig. 1). None of these birds had brood patches, so we considered them to be non-breeders or immatures migrating northward to colonies in the Bering Sea (Artukhin et al. 2010).

Genetic analysis

For genetic analysis, we mainly used 5–6 contour feathers taken from the breast or belly of live birds ($n = 55$). Feathers were dried at room temperature and stored in separate envelopes. Auklets were caught with noose carpets and mist nets installed at the colony. They were banded with numbered stainless steel bands and/or with a unique combination of three color bands, to ensure that each bird was sampled only once. Besides feathers, we also used heart or muscle samples taken from dead auklets that were killed by avian and mammalian predators (Medny, Saint-Jonah Is.; $n = 2$) or accidentally caught in salmon gillnets (in the Kuril and Kamchatka areas; $n = 41$) and preserved in ethanol (90 %). In extraction, we used tiny pieces of tissues (about $2 \times 2 \times 2$ mm). Apart from Kamchatka, most genetic samples were from presumed breeders because the birds had vascularized brood patches or had food in the

sublingual pouch. Overall, we obtained samples from five geographic locations (three with mainly or only feather samples; two with only tissue samples; Table 1).

DNA for genetic analysis was extracted using the Diatom DNA Prep 100 kit (Izogen Laboratory, Russia). All samples were minced before extraction. A 408-base pair (bp) fragment of the 3' end of the mitochondrial control region was amplified from 75 DNA samples using primers CGL-001 and CGH-549 (Kidd and Friesen 1998) in the Bio-Rad Tetrad 2 thermal cycler (Bio-Rad, USA) in 10- μ l volumes including 1x 5X Mas^{DD}TaqMIX-2025 (Dialat, Russia), 5 pM of the forward and reverse primers, 1 unit of Hot Start Taq DNA polymerase (SibEnzyme, Russia) and 1.5 μ l of DNA extract. These primers were designed specifically for mitochondrial genes but not for their nuclear copies. An initial 180-s denaturation at 94 °C was followed by 40 cycles of 94 °C for 15 s, 68 °C for 15 s and 72 °C for 15 s, and one cycle at 72 °C for 10 s. PCR products were subjected to electrophoresis through 1.5 % agarose gels and purified by alcohol precipitation. DNA was sequenced with ABI PRISM Big Dye Terminator Cycle sequencing kit v. 3.1 (Applied Biosystems, USA) following the manufacturer's protocol. All sequences were confirmed visually using chromatograms. Ambiguous sites were resolved by checking chromatograms; in few cases, ambiguous sites were unable to be resolved, so they were excluded from analysis. To ensure that PCR products did not represent contaminants, we used blank samples to control contamination during extraction and PCR. For some samples, we conducted repetitive extractions and repetitive sequencing and fragment analyses. In all cases, results were identical proving that PCR products were uncontaminated. The nuclear DNA of 97 samples was analyzed using four microsatellite loci with the primers (Apy03, Apy06, Apy07, Apy10; Dawson et al. 2005) labeled with fluorescent dyes (Apy03fam, Apy06fam, Apy07tamra, Apy10tamra). Samples were amplified following protocol from Dawson et al. (2005). We amplified samples in multiplex of the primers Apy03, Apy07 and Apy10, amplification with the primer Apy06 was carried out separately. We amplified samples for microsatellite analysis in 10- μ l volumes including 1x polymerase chain reaction buffer, 0.5 mM of each dNTP, 2.5 mM of MgCl₂, 5 pM of the forward and reverse primers, 1 unit of Hot Start Taq DNA polymerase (SibEnzyme, Russia) and 1.0 μ l of DNA extract. Microsatellite lengths were determined in an automatic genetic analyzer ABI 3500 with Liz 500 size standard using GeneMapper v. 4.0 (Applied Biosystems, USA).

Measurements of birds

We measured live birds captured with noose carpet nets or mist nets (see above) installed at the colony. For all auklets that were measured on Talan and Medny islands, we also

Table 1 Description of number and type of samples collected from each study site and used for genetic, acoustic and morphometric analysis

Site/geographic coordinates	Years of data collection/ name of collector	Genetic data		Acoustic data		Morphometric data					
		Number of genetic samples collected (feathers/tissues)	Number of mtDNA samples ^a	Number of micro-satellite samples	Num-ber of analyzed barks	Number of analyzed trumpet calls	Total number of measured birds	Birds measured at the beginning of breeding season	Birds measured at the end of breeding season	Number of measured males	Number of measured females
Talan/59.20°N 149.30°W	2008–2011/A. V. Klenova, V. A. Zubakin	20/0	20	20	50	25	221	133	88	110	111
Saint-Jonah/56.24°N 143.22°W	2009/S. P. Kharitonov	21/1	7	22							
Medny/54.40°N 167.50°W	2011–2012/A. V. Klenova, A. N. Shienok	14/1	9	14	50	25	9	0	9	5	4
Buldir/52.21°N 175.55°W	2003/V. A. Zubakin						47	29	18	18	29
Little Diomede/65.45°N 168.55°W	1999/V. A. Zubakin				50	25					
Saint Lawrence/63.30°N 170.30°W	2001–2004/V. A. Zubakin				50	25	25	0	25	10	15
Kamchatka/57.42°N 169.32°W	1997–1998/Y. B. Artukhin	0/17	16	17							
Kuril area/47.25°N 154.28°W	1997/Y. B. Artukhin	0/24	23	24							
Cape Ulaykhpent/64.23°N 173.54°W	1988–1991/ N. B. Konyukhov						200	100	100	90	110

^a GenBank Accession Nos. KJ409697–KJ409771

collected feather samples for genetic analysis (Table 1). We measured body mass with Pesola spring scales (± 1 g) and made the following linear measurements with vernier calipers (± 0.1 mm): flattened wing length, bill depth (from the proximal base of the culmen to the angle of the gonys on the underside of the bill), bill length (in dorsal aspect: from the bill tip to the edge of the feathering at the bill base), length of auricular plume and crest length (length of the longest straightened crest shaft). For analyses, we used only measurements on birds that were assumed to be adults (with vascularized brood patches or with food in sublingual pouch). Crested Auklets from Talan Island were sexed using DNA PCR analysis (Cerit and Avanus 2007); birds from other places were sexed visually according to their bill size and form, which is 98 % accurate (Jones 1993b; Klenova et al. 2012b). We measured both males and females at the beginning (2–30 June) and at the end (July 2 to August 30) of the breeding season (Table 1) and investigated relationships of season, geographic site and sex to linear measurements. Overall, we analyzed measurements from 9 to 221 auklets for each of the five sites (502 birds in total; Table 1). The majority of measurements were taken by V.A. Zubakin (all measurements from Talan, Saint Lawrence and Buldir islands; $N = 293$); measurements were also made by A.V. Klenova (Medny Island; $N = 9$) and N.B. Konyukhov (Cape Ulaykphen; $N = 200$) (Table 1).

Acoustic analysis

We recorded calls in colonies with a Marantz PMD-660 (Marantz Europe B.V., 5600 Eindhoven, Netherlands) digital recorder at a sampling frequency of 24 kHz, and an AKG-C1000S (AKG172 Acoustics GmbH, Vienna, Austria) cardioid electret condenser microphone on Talan and Medny islands. On Little Diomed and St. Lawrence islands, we used a Sony CCD-TR640E (Sony Corp., Tokyo, Japan) analog video camera, equipped with a microphone having frequency response of 0.06–12 kHz. We placed the microphone on the colony surface ~1.5–5 m from birds on Talan Island and ~2–40 m from birds on Medny Island. The distance between the video camera and birds was ~5–15 m. We recorded and analyzed calls of banded and unbanded birds. To prevent pseudoreplication, we used only 1–2 calls from banded birds (Talan) or choose for analysis calls recorded on different days, at different times, and from different parts of the colony (Medny, Little Diomed and St. Lawrence islands, where call recordings included mainly unknown birds). Overall, we obtained ~40 h of recordings.

We analyzed vocalizations with AvisoftSASLab Pro v. 5.2. (Avisoft Bioacoustics, Berlin, Germany). We produced spectrograms with the following parameters: FFT length of 1024 points, frame of 50 %, Hamming window and overlap

of 96.87 % that provides time resolution of 1.45 ms and frequency resolution of 22 Hz.

For analysis, we used the two main call types: bark and trumpet call. The bark is the most common call of Crested Auklet. It is a brief loud call, sounding like the yap of a small dog, and is performed by both sexes at the colony, at sea and in flight. It is most likely used as a contact call (Jones 1993a; Seneviratne et al. 2009; Zubakin et al. 2010). Using screen cursors, we measured the total duration, minimum, maximum and peak fundamental frequencies (Dur, $F_{\min}$, $F_{\max}$ and F_{peak} , hereafter; Fig. 2a). We analyzed 50 barks from each of the four islands (Table 1).

The trumpet call is a complex, stereotyped and individually specific vocal sequence (Fig. 2b). It is a striking advertising call in auklets that uttered mostly by males, but occasionally by females. The trumpet call consists of two parts: an introduction, which comprises 2–4 high-frequency notes, and the main part that includes alternating low- and high-frequency notes (Fig. 2b; Jones 1993a; Seneviratne et al. 2009; Zubakin et al. 2010; Klenova et al. 2011, 2012a, b). Using screen cursors, we measured 18 frequency and temporal variables on trumpet calls. These were as follows: durations of the introduction and of the main parts of the call (Dur_intr, Dur_main), duration plus minimum, maximum and peak fundamental frequencies of the longest note of the introduction (I2 note in Fig. 2b—Dur_I2, $F_{\min_I2}$, $F_{\max_I2}$, $F_{\text{peak_I2}}$); durations plus minimum and maximum fundamental frequencies of the high-frequency note following I2 (I3 note in Fig. 2b—variable abbreviations follow the preceding convention for this and the following), of the first low-frequency note (MP1 note in Fig. 2b), of the high-frequency note after MP1 (MP2 note in Fig. 2b) and of the second low-frequency note (MP3 note in Fig. 2b). We also used some derived variables: call duration (sum of durations of the introduction and main part); and note rate in the main part (duration of the main part of the call divided by the number of low-frequency notes, MP_rate). We measured 25 trumpet calls from each of the four islands (Table 1).

Statistical analysis

Genetics We carried out standard population genetic analyses in the software package Arlequin 3.5.1.2. (Excoffier and Lischer 2010). We tested for deviations from neutrality in control region variation using Ewens–Watterson (Ewens 1972; Watterson 1978) and Tajima's neutrality tests (Tajima 1989) and Chakraborty's test of population amalgamation (Chakraborty 1990). For each population, we calculated haplotypic diversity (H : Nei 1987) and nucleotide diversity (π : Tajima 1993) to estimate the level of intrapopulation genetic variation. We used the Tamura–Nei model (TrN + G+I, $I = 0.7$, $G = 0.7$) that was chosen as the most

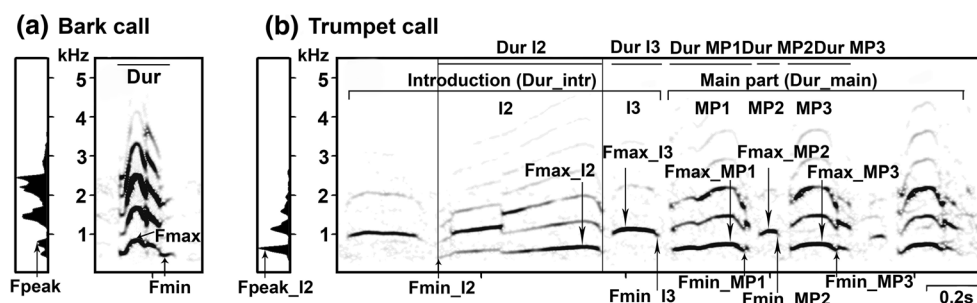


Fig. 2 Spectrogram and energetic spectrum of Crested Auklet's bark (a) and trumpet call (b). Measured acoustic variables are shown. Abbreviations for bark call: Dur—total duration; $F_{\min}$ —minimum fundamental frequency; $F_{\max}$ —maximum fundamental frequency; F_{peak} —peak fundamental frequency. Abbreviations for trumpet call: Dur_intr—duration of the introduction; Dur_main—duration of the main part of the call; Dur_I2, $F_{\min_I2}$, $F_{\max_I2}$, $F_{\text{peak_I2}}$ —duration, minimum, maximum and peak fundamental frequencies of the I2 note; Dur_I3, $F_{\min_I3}$, $F_{\max_I3}$, $F_{\text{peak_I3}}$ —duration,

minimum, maximum and peak fundamental frequencies of the I3 note; Dur_MP1, $F_{\min_MP1}$, $F_{\max_MP1}$, $F_{\text{peak_MP1}}$ —duration, minimum, maximum and peak fundamental frequencies of the MP1 note; Dur_MP2, $F_{\min_MP2}$, $F_{\max_MP2}$, $F_{\text{peak_MP2}}$ —duration, minimum, maximum and peak fundamental frequencies of the MP2 note; Dur_MP3, $F_{\min_MP3}$, $F_{\max_MP3}$, $F_{\text{peak_MP3}}$ —duration, minimum, maximum and peak fundamental frequencies of the MP3 note

suitable by the Akaike information criterion after the analysis of our data in the program Modeltest 3.7 (Posada and Crandall 1998) with invariable sites and $\gamma = 0.7$ to estimate the extent of genetic differentiation between populations (F_{ST}) with analysis of molecular variance (AMOVA). F_{ST} was tested for significance with 1000 randomizations of data. We constructed a median-joining network from genetic distances using Network 4.6.1.2 software (Bandelt et al. 1999).

We estimated the degree of polymorphism observed in microsatellite sequences by calculating number of alleles, observed and expected heterozygosity, polymorphism information content (PIC) and carrying out the exact test of deviations from Hardy–Weinberg equilibrium using the software package CERVUS 3.0.3 (Kalinowski et al. 2007). We calculated R_{ST} and F_{ST} between microsatellite loci and their significance ($P < 0.017$ after BY-correction) with AMOVA in Arlequin 3.5.1.2. To estimate the level of genetic differentiation between populations, we run Bayesian population clustering analysis with the admixture model which assumed mixing of specimens from different populations and correlated allele frequencies model (length of burnin period is 100,000, the number of MCMC repeats after burnin is 1,000,000) in the software package STRUCTURE 2.3.4. (Pritchard et al. 2000). We calculated optimal value of K (number of genetic clusters) following the protocol from the software documentation with the number of iteration equals to 5 and $K = 1$ –10 (Pritchard et al. 2000). Also we carried out Bayesian population clustering analysis with the LOCPRIOR model that uses sampling locations as a prior.

Body measurements and vocalizations Analyses of body measurements and acoustic variables were carried out with the statistical package STATISTICA 8.0 (StatSoft, Tulsa, OK, USA). All tests were two-tailed; all means are given

as mean $\pm$ SD, and differences were considered significant where $P < 0.05$. Since the distribution of residuals for all measured variables did not differ from normality assumption for each geographic site ($P > 0.05$, Kolmogorov–Smirnov test) and Levene's tests were used to verify the homocasticity assumption in ANOVA analyses, we could apply ANOVA and MANOVA. In both analyses, we first carried out one-way ANOVA with Tukey HSD post hoc test to estimate the influence of the factor on each response variable and to compare the variable values across sites. Then we conducted MANOVA to evaluate factor's influence on all response variables together. We used Pillai's trace as the most robust of the test statistics for the MANOVA as recommended in Quinn and Keough (2002). In morphometric analyses, we also conducted the main-effect ANOVA to study the influence of factors "site," "sex" and "season" on response variables. We used the Benjamini–Yekutieli correction of false discovery rate (Narum 2006) to determine statistical significance of our multivariable analyses. After BY-correction, the levels of significance for different analyses were the following: α (genetic analyses) = 0.017, α (morphometric analysis) = 0.02, α (bark analysis) = 0.024, α (trumpet call analysis) = 0.014.

Results

Genetics

Nuclear copies of mitochondrial genes have been reported in other seabirds, but the received auklet sequences did not differ from the patterns expected for true mtDNA (Kidd and Friesen 1998; Friesen et al. 2005; Birt et al. 2011). Sequences (408 bp) were similar to those of the

Table 2 Genetic polymorphism in the control region's fragment of Crested Auklets from different geographic sites

	Talan	Kamchatka	Kuril area	Medny	St.-Jonah
Number of samples	20	16	23	9	7
Number of haplotypes	20	16	23	9	6
Number of polymorphic sites	26	25	25	18	22
Number of substitutions	26	25	26	18	22
Number of transitions	25	23	23	18	21
Number of transversions	1	2	3	0	1
Number of insertions/deletions	0	0	1	0	0
π	0.013 $\pm$ 0.008	0.013 $\pm$ 0.008	0.013 $\pm$ 0.008	0.012 $\pm$ 0.008	0.019 $\pm$ 0.012
H	1.000 $\pm$ 0.016	1.000 $\pm$ 0.022	1.000 $\pm$ 0.013	1.000 $\pm$ 0.052	0.952 $\pm$ 0.096

Table 3 Values of corrected genetic distances (F_{ST} , Tamura–Nei model +G+I) between Crested Auklets from different geographic sites based on the mitochondrial control region fragment; their P values are given in brackets, confidence level after BY-correction $P = 0.017$

	Talan I.	Kamchatka	Kuril area	Medny I.	St.-Jonah I.
Talan I.					
Kamchatka	0.015 ($P = 0.20$)				
Kuril area	0.006 ($P = 0.28$)	−0.009 ($P = 0.61$)			
Medny I.	0.053 ($P = 0.04$)	−0.001 ($P = 0.45$)	0.016 ($P = 0.25$)		
St.-Jonah I.	0.038 ($P = 0.12$)	0.048 ($P = 0.07$)	0.052 ($P = 0.06$)	0.025 ($P = 0.23$)	

Birds from Kamchatka are non-breeders

mitochondrial control region of other alcids, a poly-C repeat occurred at the 5' end of the control region, and base composition was biased against Gs (30.1 % A, 29.8 % C, 14.7 % G, 25.6 % T). We found that almost every haplotype was unique for a single population. Only three haplotypes occurred more than once: haplotype t84 was shared between Talan Island and Kuril area, haplotype k11 was shared between Kuril area and Medny Island, and haplotype i13 was found only in two specimens from Saint-Jonah Island. Data and statistics are summarized in Table 2. We found no evidence of deviations from neutrality of the chosen fragment (Ewens–Watterson and Chakraborty's tests, $P = 0.76$ –1.00) and found significant genetic differences only between birds from Talan and Medny (Table 3), but after BY-correction, this difference became insignificant ($P > 0.017$). In the median network, we found no genetic groups (Fig. 3).

All four microsatellite loci were polymorphic. They did not deviate significantly from the Hardy–Weinberg equilibrium (Table 4). Data and statistics on allelic frequencies by site are summarized in the Supplemental Material. We calculated the indices of genetic differentiation (F_{ST} and R_{ST}), which showed the absence of any significant differences between colonies (Table 5). There were two exceptions: the pairs Talan–Medny ($F_{ST} = 0.058$, $P < 0.017$) and Talan–Kuril area ($F_{ST} = 0.037$, $P < 0.017$), but F_{ST} values were low and

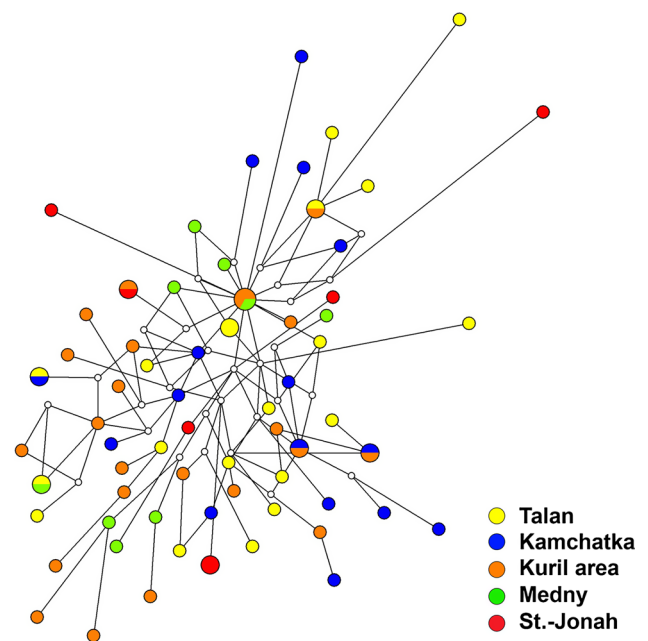
**Fig. 3** Median-joining network of mtDNA haplotypes of Crested Auklets. Branch length is proportional to the number of mutations, circle diameter is proportional to the number of birds with this haplotype. Different colors mean haplotypes found in different colonies. The smallest white circles are median vectors

Table 4 Characterization of microsatellite loci: number of alleles, observed (Ho) and expected (He) heterozygosity, polymorphism information content (PIC) and results of tests for deviations from Hardy–Weinberg equilibrium (HW)

Microsatellite locus	Number of alleles	Ho	He	PIC	HW
Apy03	15	0.68	0.77	0.74	NS ^a
Apy06	18	0.80	0.91	0.90	ND ^a
Apy07	10	0.74	0.79	0.75	NS
Apy10	14	0.84	0.82	0.80	NS
Average	14.25	0.77	0.82	0.80	

^a NS not significant; ND not performed

R_{ST} did not support these differences ($R_{ST} = -0.03$, $P = 0.87$ and $R_{ST} = -0.01$, $P = 0.5$, respectively). Results of Bayesian population clustering analysis in STRUCTURE confirmed these results. An optimal value of genetic clusters was $K = 1$ with probability $P = 0.37$. Usage of the LOCPRIOR model did not change the results ($K = 1$, $P = 0.37$).

Measurements of birds

The factor “sex” had the strongest influence on variability of all morphometric variables (MANOVA, $F = 252.6$, $P < 0.05$). Males were significantly heavier and had significantly greater wing length, bill length and bill depth than females (Table 6; Fig. 4c). The factor “season” affected significantly only the body mass and length of auricular plume of Crested Auklets. At the beginning of the breeding season (June), Crested Auklets were heavier and had longer auricular plumes than at the end of the season (July, August) (Table 6; Fig. 4b). We found that three of six morphometric variables (body mass, bill length and bill depth) differed significantly between geographic sites (Table 6). The auklets from Talan Island were heavier than auklets from all other study sites. Auklets from Cape Ulaykphen had the longest and deepest bills than auklets from all other studied sites (Table 6; Fig. 4a). At the same time, comparison of ANOVA F -ratios showed that the effect of the season or

sex on morphometric variables was always much stronger than the effect of geographic site (Table 6). MANOVA showed the same results: $F(\text{season}) = 21.9$, $F(\text{sex}) = 252.6$ while $F(\text{site}) = 17.03$ ($P < 0.05$ for both values).

Vocalizations

The factor “site” had a slight but significant effect on variability of three (of four total) acoustic variables of barks (Table 7; Fig. 5a). Only the maximum fundamental frequency (F_{max}) of barks did not differ between colonies ($P = 0.29$). However, the remaining three variables differed only between barks recorded on Talan Island and the other three island colonies. Crested Auklet barks recorded on Talan Island were lower in minimum and peak fundamental frequencies (F_{min} and F_{peak}) and longer in duration (Dur) than barks recorded on Little Diomedé, St. Lawrence, and Medny islands (Table 7). But the values of all measured variables overlapped greatly and the influence of the “site” was not so strong on all response variables together, although significant (MANOVA, $F = 6.6$, $P < 0.05$).

The factor “site” had a significant effect on five of twenty measured temporal-frequency variables of trumpet call (Table 7; Fig. 5b). As in the case of barks, trumpet calls recorded on Talan Island were lower in MP1 maximum fundamental frequency ($F_{\text{max_MP1}}$) than trumpet calls recorded on other three islands. Also, calls from Talan birds had longer introduction (Dur_intr) than calls from Medny and St. Lawrence islands, and longer I2 note (Dur_I2) than calls from St. Lawrence Island. Trumpet calls of birds from Talan and Little Diomedé islands had lower I3 minimum fundamental frequency ($F_{\text{min_I3}}$) than calls recorded on Medny and St. Lawrence islands. In addition, the I3 maximum fundamental frequency ($F_{\text{max_I3}}$) of calls from Medny Island was higher than that of calls from Little Diomedé Island. However, F -values of one-way ANOVA were low in all these cases, and the values of all measured variables overlapped greatly (Table 7). The results of MANOVA also showed significant influence of “site” on trumpet call variables, although the F -value was very low ($F = 2.8$, $P < 0.05$).

Table 5 Values of corrected genetic distances (F_{ST} , Tamura–Nei model +G + I) (above the diagonal) and average genetic distances R_{ST} (under the diagonal) between Crested Auklets from different geographic sites based on microsatellite length, and their P values are given in brackets

	Talan I.	Kamchatka	Kuril area	Medny I.	St.-Jonah I.
Talan I.		0.004 ($P = 0.29$)	0.037* ($P = 0.004$)	0.058* ($P = 0.000$)	0.005 ($P = 0.29$)
Kamchatka	−0.01 ($P = 0.7$)		0.001 ($P = 0.35$)	0.024 ($P = 0.07$)	−0.015 ($P = 0.96$)
Kuril area	−0.01 ($P = 0.5$)	−0.02 ($P = 0.81$)		0.031 ($P = 0.02$)	0.007 ($P = 0.15$)
Medny I.	−0.03 ($P = 0.87$)	−0.03 ($P = 0.84$)	−0.01 ($P = 0.6$)		0.03 ($P = 0.023$)
St.-Jonah I.	−0.01 ($P = 0.59$)	−0.03 ($P = 0.99$)	−0.02 ($P = 0.88$)	−0.03 ($P = 0.91$)	

Birds from Kamchatka are non-breeders

* significant difference, $P < 0.017$ (after BY-correction)

Table 6 Descriptive statistics (mean $\pm$ SD) and main effect ANOVA results (F ratio and P values) for effects of the site, sex and season on morphometric variable values in the Crested Auklet

	N	Body mass (g)	Wing length (mm)	Bill length (mm)	Bill height (mm)	Crest length (mm)	Auricular plume length (mm)
Talan	221	276 $\pm$ 23	143.7 $\pm$ 3.8	12.2 $\pm$ 0.7	11.7 $\pm$ 1.1	38.8 $\pm$ 5.6	27.5 $\pm$ 4.1
Medny	9	243 $\pm$ 16	144.8 $\pm$ 4.0	11.9 $\pm$ 0.6	11.5 $\pm$ 0.8	41.7 $\pm$ 4.1	26.0 $\pm$ 3.7
Buldir	47	255 $\pm$ 16	141.8 $\pm$ 3.2	11.7 $\pm$ 0.8	11.2 $\pm$ 0.9	39.8 $\pm$ 5.7	29.2 $\pm$ 4.5
St. Lawrence	25	260 $\pm$ 19	143.0 $\pm$ 4.0	12.2 $\pm$ 0.6	11.7 $\pm$ 0.9	–	–
Cape Ulaykhpen	200	259 $\pm$ 22	143.9 $\pm$ 4.1	12.3 $\pm$ 0.7	12.2 $\pm$ 1.0	–	–
Effect of “site” (main-effect ANOVA)	$F_{4,495}$	21.9	2.7	10.99	46.8	1.3	3.9
	P	$P < 0.02$	$P = 0.030$	$P < 0.01$	$P < 0.02$	$P = 0.266$	$P = 0.021$
June	262	274 $\pm$ 23	143.4 $\pm$ 3.8	12.2 $\pm$ 0.7	12.0 $\pm$ 1.1	38.7 $\pm$ 5.7	28.4 $\pm$ 4.1
July–August	240	256 $\pm$ 20	143.7 $\pm$ 4.1	12.2 $\pm$ 0.7	11.7 $\pm$ 1.1	39.6 $\pm$ 5.4	26.8 $\pm$ 4.2
Effect of “season” (main-effect ANOVA)	$F_{1,495}$	62.2	4.3	0.3	6.0	1.7	7.8
	P	$P < 0.02$	$P = 0.038$	$P = 0.586$	$P < 0.02$	$P = 0.199$	$P < 0.02$
Males	232	276 $\pm$ 23	145.1 $\pm$ 3.7	12.5 $\pm$ 0.7	12.8 $\pm$ 0.7	39.7 $\pm$ 5.7	28.3 $\pm$ 4.1
Females	270	257 $\pm$ 21	142.3 $\pm$ 3.7	11.9 $\pm$ 0.6	11.1 $\pm$ 0.7	38.5 $\pm$ 5.5	27.3 $\pm$ 4.3
Effect of “sex” (main-effect ANOVA)	$F_{1,495}$	81.6	73.0	98.1	1013.3	3.5	4.1
	P	$P < 0.02$	$P < 0.02$	$P < 0.01$	$P < 0.02$	$P = 0.063$	$P = 0.044$

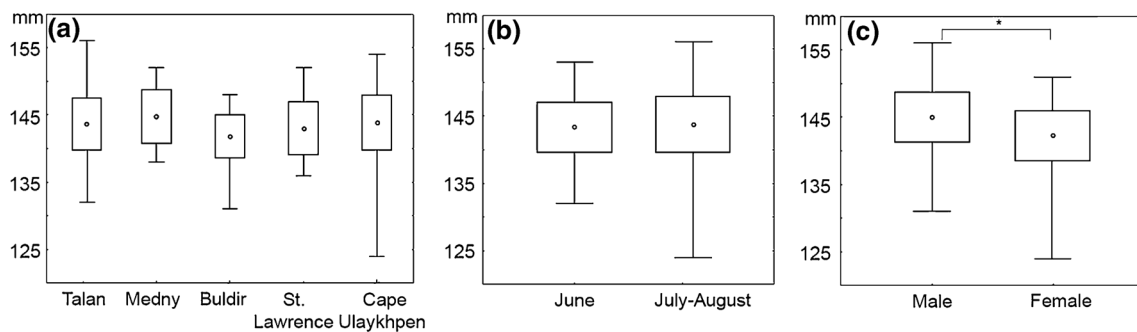


Fig. 4 Differences in wing length of Crested Auklets between different colonies (a), different seasons (b) and different sexes (c). Asterisk (*) means significant differences after Benjamini–Yekutieli correction

($P < 0.02$). The middle points show means; box—SD; whiskers—minimum and maximum values

Discussion

We analyzed geographic variability in Crested Auklet and found no obvious patterns that suggest population differentiation in genetics, body size, feather length or vocalizations.

Almost all studied haplotypes were unique and differed only in 1–2 substitutions. Examined Crested Auklets were characterized by relatively high haplotypic ($H_{\text{mean}} = 0.99 \pm 0.22$) and low nucleotide diversity ($\pi_{\text{mean}} = 0.014 \pm 0.008$). Similar results on control region variation (high haplotypic and low nucleotide diversity) were shown on other colonial seabirds (for instance, Red-legged kittiwake (*Rissa brevirostris*; Patirana et al. 2002), Band-rumped Storm petrel (*Oceanodroma castro*; Smith et al. 2007); Ancient Murrelet (*Synthliboramphus antiquus*; Pearce et al. 2002)).

We did not find significant interpopulation differences between geographic sites of Crested Auklets in considered sequences of control region’s fragment and microsatellite loci. All results of genetic analysis point to a lack of isolation among colonies. Correspondence between mtDNA and nuclear DNA results could indicate the lack of isolation in recent and historic times, or of recent (post-Pleistocene) isolation or of secondary contact. Adults show strong nest-site fidelity between years (~70–75 % of breeders returned to the same nest chambers between years and some nested 0.3–3.6 m from the previous year’s nest site; Zubakin 1990; Fraser et al. 2004; Jones et al. 2004; Klenova et al. 2012a). Therefore, genetic exchange among colonies must occur mainly through juvenile dispersal.

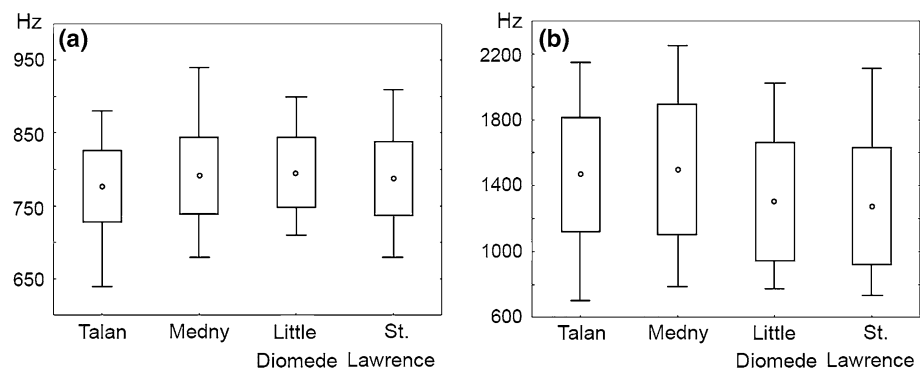
Among other Alcidae species, distinctive populations were also not found in Ancient Murrelet (Pearce et al. 2002), Dovekie (*Alle alle*; Wojczulanis-Jakubas et al. 2014)

Table 7 Descriptive statistics (mean $\pm$ SD) and results of one-way ANOVA (F ratio and *P* values) for the site effects on some of acoustic variable values Crested Auklet's barks and trumpet calls

	Acoustic variables	Talan	Medny	Little Diomed	St. Lawrence	Effect of "site" (one-way ANOVA)
Bark call (<i>N</i> = 50)	Dur (ms)	0.16 $\pm$ 0.03 ^a	0.14 $\pm$ 0.02 ^b	0.15 $\pm$ 0.03 ^{a, b}	0.14 $\pm$ 0.02 ^b	$F_{3,196} = 8.0$ $P < 0.024$
	<i>F</i> _{max} (Hz)	776.8 $\pm$ 49.8 ^a	791.4 $\pm$ 52.7 ^a	795.4 $\pm$ 48.0 ^a	786.8 $\pm$ 50.4 ^a	$F_{3,196} = 1.7$ $P = 0.285$
	<i>F</i> _{peak} (Hz)	721.0 $\pm$ 53.7 ^a	748.6 $\pm$ 59.6 ^{a, b}	759.6 $\pm$ 46.6 ^b	749.6 $\pm$ 50.2 ^{a, b}	$F_{3,196} = 4.93$ $P < 0.024$
Trumpet call (<i>N</i> = 25)	Dur _{intr} (ms)	0.945 $\pm$ 0.396 ^a	0.756 $\pm$ 0.205 ^b	0.853 $\pm$ 0.276 ^{a, b}	0.664 $\pm$ 0.148 ^b	$F_{3,246} = 5.0$ $P < 0.014$
	Dur _{I2} (ms)	0.476 $\pm$ 0.089 ^a	0.512 $\pm$ 0.138 ^{a, b}	0.545 $\pm$ 0.180 ^{a, b}	0.410 $\pm$ 0.123 ^b	$F_{3,246} = 4.5$ $P < 0.014$
	<i>F</i> _{max_I2} (Hz)	1548 $\pm$ 376 ^a	1514 $\pm$ 349 ^a	1362 $\pm$ 375 ^a	1293 $\pm$ 364 ^a	$F_{3,246} = 2.8$ $P = 0.047$
	<i>F</i> _{min_I3} (Hz)	804 $\pm$ 127 ^a	889 $\pm$ 151 ^b	757 $\pm$ 118 ^a	868 $\pm$ 151 ^b	$F_{3,246} = 4.8$ $P < 0.014$
	<i>F</i> _{max_I3} (Hz)	1395 $\pm$ 129 ^{a, b}	1413 $\pm$ 121 ^a	1299 $\pm$ 120 ^b	1414 $\pm$ 130 ^{a, b}	$F_{3,246} = 4.9$ $P < 0.014$
	Dur _{main} (ms)	1.233 $\pm$ 0.542 ^a	1.051 $\pm$ 0.406 ^a	1.310 $\pm$ 0.406 ^a	1.322 $\pm$ 0.382 ^a	$F_{3,246} = 2.0$ $P = 0.114$
	Dur _{MP1} (ms)	0.295 $\pm$ 0.010 ^a	0.264 $\pm$ 0.072 ^a	0.280 $\pm$ 0.113 ^a	0.237 $\pm$ 0.049 ^a	$F_{3,246} = 2.0$ $P = 0.118$
	<i>F</i> _{max_MP1} (Hz)	815 $\pm$ 88 ^a	853 $\pm$ 60 ^b	860 $\pm$ 55 ^b	852 $\pm$ 52 ^b	$F_{3,246} = 6.5$ $P < 0.014$
	<i>F</i> _{max_MP2} (Hz)	1327 $\pm$ 220 ^a	1345 $\pm$ 180 ^a	1283 $\pm$ 169 ^a	1374 $\pm$ 143 ^a	$F_{3,246} = 1.1$ $P = 0.351$
	Dur _{MP3} (ms)	0.239 $\pm$ 0.067 ^a	0.216 $\pm$ 0.046 ^a	0.231 $\pm$ 0.025 ^a	0.214 $\pm$ 0.021 ^a	$F_{3,246} = 1.9$ $P = 0.134$
	<i>F</i> _{max_MP3} (Hz)	853 $\pm$ 39 ^a	871 $\pm$ 52 ^a	899 $\pm$ 47 ^a	860 $\pm$ 56 ^a	$F_{3,246} = 2.6$ $P = 0.05$
	Dur _{total} (ms)	2.146 $\pm$ 0.619 ^a	1.856 $\pm$ 0.420 ^a	2.163 $\pm$ 0.515 ^a	1.986 $\pm$ 0.374 ^a	$F_{3,246} = 2.2$ $P = 0.096$

^{a, b} Values that did not differ significantly are indicated by the same superscripts ($P > 0.024$ for barks, $P > 0.014$ for trumpet calls, Tukey HSD post hoc test)

Fig. 5 Differences in bark maximum fundamental frequency (a) and maximum fundamental frequency of trumpet call I2 note (b) of Crested Auklets from different colonies. The middle points show means; box—SD; whiskers—minimum and maximum values



and Common Murre (*Uria aalge*; Moum and Arnason 2001). In contrast, different genetic groups among alcids were reported for Cassin's Auklet (*Ptychoramphus aleuticus*; Wallace et al. 2015), Marbled Murrelet (*Brachyrhamphus marmoratus*; Friesen et al. 2005; Vásquez-Carrillo et al. 2014), Kittlitz's Murrelet (*Brachyrhamphus brevirostris*; Birt et al. 2011), Rhinoceros Auklet (*Cerorhinca monocerata*; Abbott et al. 2014) and Razorbill (*Alca torda*; Moum and Arnason 2001). Long-billed Murrelet (*Brachyrhamphus perdix*) is considered to be an example of cryptic species (Friesen et al. 1996b). An objective interspecific comparison is possible only in the case of similar markers used in different studies, but apart from results of Vásquez-Carrillo et al. (2014), all of the above-mentioned analyses were made on a few different neutral markers (mitochondrial control region, microsatellites or nuclear introns), making this comparison relevant.

Morphometric variability showed that sex and season features affect body mass and most of the linear characteristics of adult Crested Auklets much more strongly than geographic location. We did not find a significant effect of geographic site on the wing, crest and auricular plume lengths. Other morphometric variables differ slightly but significantly between birds from different sites. We assumed that such slight differences in morphometric variables could reflect ecological peculiarities of colonies, especially variability in forage conditions and the demographic structure of breeding population. For instance, Crested Auklet body mass could depend on the distance from a breeding colony to feeding place and on the plankton concentration there (N.B. Konyukhov, pers comm). Besides, it has been shown that ornament expression and rectal plate size can increase with age (Jones et al. 2000). Thus, morphometric differences found in our study

might reflect age- or ecology-dependent (but not genetic-dependent) differences between populations. Also, the morphometric differences found in the present study may reflect some impact of individual researchers. Indeed, in our analysis we used data obtained by different researchers who work on different islands (Talan, Saint Lawrence and Buldir—V.A. Zubakin; Medny—A.V. Klenova; Cape Ulaykphen—N.B. Konyukhov; Table 1). It is well known that measurer effects can be very large (e.g., different people could apply slightly different pressure to the calipers), and we may expect the artificial impression of population differences in our results. However, in spite of this, the effect of geographic site on the majority of variables found in the present study was very weak or even insignificant. So we can suggest that morphometric population variability is poorly expressed in Crested Auklet.

In some other alcids, morphometric population variability was reported while in others it could not be detected. For example, Whiskered Auklet, a closely related species, shows extreme inter-population differences in morphometric characteristics (Feinstein 1959; Klenova et al. 2013). Differences in body mass and tarsus length are so large that different populations do not overlap at all (Klenova et al. 2013). Strong differences in morphological features have been reported also for Common and Thick-billed Murres (*Uria lomvia*), and Black (*Cepphus grille*) and Pigeon (*C. columba*) Guillemots (Gaston and Jones 1998). Atlantic Puffin (*Fratercula arctica*) and Dovekie also display some geographic variability in size (Gaston and Jones 1998; Wojczulanis-Jakubas et al. 2011). In contrast, significant geographic variability in size has not been found for Parakeet (*Cyclorhynchus psittacula*) and Least (*Aethia pusilla*) Auklets and also for Horned (*Fratercula corniculata*) and Tufted (*F. cirrhata*) Puffins (Gaston and Jones 1998).

The bark call exhibited geographic variation in three of four measured acoustic variables. Birds from Talan Island differed from birds at other colonies, but those colonies did not differ from one another. Barks of the Crested Auklets from Talan Island had the lowest minimum and peak fundamental frequencies and were the longest. However, we suppose that such small differences could be explained mostly with physiological and ecological factors, rather than isolation. Particularly, we found that birds from Talan Island were also the heaviest among four other studied Crested Auklet populations. Previously the correlation between fundamental call frequency and body condition (but not body size) has been shown for Crested Auklet (Klenova et al. 2011), and also for some other non-passerine species (e.g., Appleby and Redpath 1997; Miyazaki and Waas 2003; Hardouin et al. 2007; Mager et al. 2007). In all listed cases, lower-frequency calls indicate heavier (but not bigger) males and hence reflect the current condition of the caller. Interestingly, in the second analyzed call type, in

trumpet call, we also noted the same tendency. Thus, trumpet calls recorded on Talan Island were lower in MP1 maximum fundamental frequency ($F_{\text{max_MP1}}$) and longer in introduction (Dur_intr) and I2 note (Dur_I2) than calls recorded on the other three islands. In general, in contrast to contact calls (barks), the trumpet calls of Crested Auklets are important in mate choice and some other social interactions between conspecifics (Jones 1993a; Zubakin et al. 2010). So as sexually selected signals, they should be more sensitive markers of population divergence than barks (Soha et al. 2004; Wright et al. 2005; Alstrom et al. Alström et al. 2007; Smith and Friesen 2007). However, we found significant differences in only five of twenty variables measured in Crested Auklet trumpet calls from different colonies. The differences were slight, so our results could once again argue against distinct isolation between populations. However, the prominent individual specificity of the trumpet call has been previously reported (Klenova et al. 2011, 2012a). Therefore, we suppose that huge individual variability could in some degree mask a weaker effect of geographic site on acoustic variables of advertising call in this species.

Population variability of acoustic parameters has been studied thoroughly for a very few seabird species, all of which demonstrated well-expressed population differentiation. These studies show that if genetic and/or morphometric differences between seabird populations exist, there are also differences in their vocalizations (e.g., Whiskered Auklet, Klenova et al. 2013; Band-rumped Storm petrel, Smith and Friesen 2007; Wilson's Storm Petrel *Oceanites oceanicus*, Bretagnolle 1989).

In summary, our study suggests that there is little or no geographic structuring, genetically or in body size, plumage traits or vocalizations, in the Crested Auklet. This conclusion agrees with recent information about adult Crested Auklet winter movements obtained with the help of geolocators. Outside the breeding season, Crested Auklets can travel throughout the whole species' range and show no obvious migratory routes (Robinson and Jones 2013). We suppose that young birds can join adult flocks and travel widely throughout the Bering and Okhotsk seas, as well as adjacent waters of the North Pacific. In spring, young birds can be found far from their natal colonies. They presumably choose their first breeding site at the age of 2–3 years and show high breeding-site fidelity thereafter (see above).

In contrast to Crested Auklets, Whiskered Auklet colonies seem to be well isolated from one another (Feinstein 1959; Klenova et al. 2013). Comparison of these two species provides insights into principles of population differentiation. Breeding colonies of the Whiskered Auklet usually are located in ice-free areas, overlapping with the most southern Crested Auklet colonies (Gaston and Jones 1998). This factor could allow Whiskered Auklets to stay near

colonies year-round. During the breeding season, Whiskered Auklets feed up to ~ 16 km offshore, in tidal convergences, tidal pumps and areas of standing waves of up to 10 m amplitude (Byrd and Williams 1993; Gaston and Jones 1998; Zubakin and Konyukhov 2001). On the contrary, feeding trips of Crested Auklets are up to 100 km long and the adults feed in parts of the water column that are stratified and have dense concentrations of zooplankton, especially in areas with strong currents, tide rips and upwelling transport (Gaston and Jones 1998). Therefore, Crested Auklets, especially in northern colonies, are likely to move much more than Whiskered Auklets over the annual cycle. Finally, among alcids only Whiskered Auklet fledglings return to the native colony soon after fledging (Konyukhov and Zubakin 1994; Zubakin and Konyukhov 2001).

Other seabird species display similar patterns. Population differentiation in guillemots (*Cephus*) is stronger than in murres (*Uria*), in agreement with differences in movements. Indeed, guillemots breed in small colonies and often stay close to them year-round, whereas murres breed in large colonies and migrate seasonally (Taylor and Friesen 2012). Black-browed (*Thalassarche melanophris*) and Gray-headed Albatrosses (*T. chrysostoma*) provide a similar example. The former is neritic and forages near colonies; the latter is oceanic one and forages far from colonies (Burg and Croxall 2001). To sum up, the absence of distinctive populations in Crested Auklets can be explained by their dispersal behavior: They are pelagic and forage along frontal systems, so that young birds are likely to migrate far away from their natal colonies during the first year of life.

It would be useful to expand our data with measurements of all types from colonies which were not involved in present analysis. Nevertheless, we suppose that our results are quite representative.

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