ISSN 1062-3590, Biology Bulletin, 2015, Vol. 42, No. 7, pp. 674–681. © Pleiades Publishing, Inc., 2015.
Original Russian Text © O.A. Filatova, E.A. Borisova, O.V. Shpak, I.G. Meschersky, A.V. Tiunov, A.A. Goncharov, I.D. Fedutin, A.M. Burdin, 2014, published in Zoologicheskii Zhurnal, 2014, Vol. 93, No. 11, pp. 1345–1353.

Reproductively Isolated Ecotypes of Killer Whales *Orcinus orca* in the Seas of the Russian Far East[1]

O. A. Filatova[a], E. A. Borisova[a], O. V. Shpak[b], I. G. Meschersky[b], A. V. Tiunov[b], A. A. Goncharov[b], I. D. Fedutin[a], and A. M. Burdin[c]

[a] *Faculty of Biology, Moscow State University, Moscow, 119992 Russia*
[b] *Severtsov Institute of Ecology and Evolution RAS, Moscow, 119071 Russia*
[c] *Kamchatka Branch of Pacific Institute of Geography FEB RAS, Petropavlovsk-Kamchatsky, 683024 Russia*
e-mail: alazor@rambler.ru

Received June 11, 2013

Abstract—Two ecotypes of killer whales—fish-eating and mammal-eating—have been found in the seas of the Russian Far East, but confirmation of their status required genetic studies of animals with known phenotype and foraging specialization. In this paper we combine the results of the analysis of nuclear genetic markers, isotopic composition of tissues and phenetic feature (shape of the saddle patch) of killer whales from different regions of Far Eastern seas. Analysis of allelic composition of 9 microsatellite loci of the nuclear DNA divided the samples into two distinct clusters with the divergence between them high enough to indicate reproductive isolation. The content of nitrogen stable isotope ^{15}N in tissues of whales from the first cluster was significantly lower than that of the second cluster. The difference of $\delta^{15}N$ values between individuals from different clusters was about 3‰, which corresponds to the difference between adjacent trophic levels. Apparently, the first cluster comprised fish-eating, and the second—mammal-eating animals. The ratio of saddle patch shape types also differed between the clusters. Whales from the first cluster had five types of patch shape in different proportions, while whales from the second cluster had only "smooth" saddle patches. The differences between the clusters were statistically significant. Thus, killer whales from the seas of the Russian Far East comprise at least two reproductively isolated clusters with stable ecological and morphological differences, that is, two different ecotypes—fish-eating and mammal-eating. Different ecotypes of killer whales should be managed separately during abundance surveys, monitoring, evaluation of human impact and estimates of total allowed takes from the wild populations.

Keywords: killer whale, *Orcinus orca*, ecotypes, foraging specializations

DOI: 10.1134/S1062359015070043

INTRODUCTION

Killer whale (*Orcinus orca*) is a predator with a wide ecological niche (Ford, 2002), but separate populations often specialize on a particular type of prey (Ford et al., 1998; Saulitis et al., 2000). For example, in the waters of the Pacific coast of North America three ecotypes occur that differ in foraging specialization as well as behavior, social structure and some morphological features (Ford, 2002). In the coastal waters two of these three ecotypes are common: fish-eating (so-called "resident") and mammal-eating (so-called "transient"). Fish-eating killer whales mostly feed on salmon and other fish species, while mammal-eaters hunt on marine mammals—seals, dolphins, porpoises and even large whales (Ford et al., 1998; Saulitis et al., 2000). Differences in foraging specialization lead to the differences in behavior, social structure and morphology. Fish-eating killer whales live in families. A family consists of a female and several generations of her offspring; both sexes stay in the natal group for their entire lives (Bigg et al., 1990). In mammal-eating killer whales, some animals leave their family at the age of maturity, because it is harder to hunt in large groups as seals can detect them more easily. Mammal-eating killer whales also differ from fish-eaters by the more robust skull (Krahn et al., 2004), as well as by the shape of the dorsal fin and the saddle patch (Baird and Stacey, 1988).

Besides two coastal ecotypes, pelagic or "offshore" killer whales occur in the north-eastern Pacific; they usually travel offshore and rarely approach the coast. Because of this, they are yet poorly studied; it is known that they often travel in large groups and probably specialize in feeding on sharks (Ford et al., 2011).

Different killer whale ecotypes were also described in Antarctic waters. At least four easily distinguishable ecotypes are recognized there to date. Type "A" killer whales hunt mostly on minke whales (*Balaenoptera acutorostrata*) in ice-free areas (Pitman and Ensor, 2003). Two ice-associated ecotypes—"B" and "C"—

[1] The article was translated by the authors.

differ considerably from "A" type and all other killer whales by their coloration: they are not black but grey, with slightly darker dorsal area (Pitman and Ensor, 2003). Type "B" killer whales hunt on seals, which haul out on the ice floes drifting around Antarctica. They are large animals with huge eye patch that makes them easily recognizable (Pitman and Ensor, 2003). Type "C" killer whales are fish-eaters, feeding mostly on Antarctic toothfish (*Dissostichus mawsoni*). They are smaller than other forms and have narrow slanting eye patch (Pitman and Ensor, 2003). The fourth sub-Antarctic "D" type is known only from a few encounters; the data about this type is scarce, but it has a distinctive appearance: tiny eye patch, bulbous head (similar to a pilot whale) and small dorsal fin (Pitman et al., 2010).

Killer whales from the different ecotypes do not interbreed in the wild, which leads to a substantial genetic differentiation (Hoelzel and Dover, 1991). Analysis of the complete sequences of mitochondrial DNA has shown that the North Pacific mammal-eating "transient" ecotype is the most divergent clade—it separated from the common ancestor more than 700 thousand years ago (Morin et al., 2010). Antarctic killer whales are also quite different from the other populations—the time of their divergence is estimated around 150 thousand years ago. North Pacific fish-eating killer whales were found to be more closely related to the North Atlantic killer whales, than to sympatric North Pacific mammal-eaters (Morin et al., 2010).

In Russian waters, the occurrence of two forms of killer whales was demonstrated, one similar in morphology and behavior to the fish-eating "resident", and another—to the mammal-eating "transient" killer whales from Pacific North American waters (Burdin et al., 2004; Ivkovich et al., 2010). Analysis of the control region of the mitochondrial DNA has confirmed that the "fish-eating" and "mammal-eating" killer whales from the Russian waters are related to the North American fish- and mammal-eating populations (Burdin et al., 2004). However, mitochondrial DNA conveys information only on the maternal relatedness; so it remained unknown if fish- and mammal-eating killer whales interbreed in the Russian waters or represent reproductively isolated populations. To clarify this, the analysis of nuclear DNA was essential. Besides, the observations of foraging events of presumed fish-eating and mammal-eating animals could not exclude the possibility that they sometimes switched to another prey type. More precise method to study the feeding habits is stable isotope analysis of tissues that allows determining the trophic level of an animal.

In this paper we combine the results of genetic analysis, analysis of nitrogen stable isotope composition ($^{15}N/^{14}N$) and analysis of phenetic feature (saddle patch shape) of killer whales from different regions of Far Eastern seas to clarify the question of presence of fish-eating and mammal-eating ecotypes of killer whales in the Russian waters.

MATERIALS AND METHODS

The main data used for this work were 67 biopsy samples of killer whales from four regions: Avacha Gulf (41 samples) and Karaginsky Gulf (2 samples) of Kamchatka peninsula, Commander Islands (11 samples) and western Okhotsk Sea (Academia Gulf) (13 samples) (Fig. 1).

Samples were obtained with a crossbow using a special arrow tipped with a sharp-edged metal tube. This tube penetrates 1.5–2 cm into the whale's skin and blubber, while the plastic float ("stopper") on the arrow damps the stroke and pushes the arrow back. The piece of skin and blubber stays in the arrow tip. Biopsied whales were photographed for the subsequent photoidentification. We used these photographs to analyze the saddle patch shape.

Two samples from the Commander Islands were collected from stranded animals. The first sample was from a dead female found in Buyan Bay on Bering Island on January 27, 2007. This sample was kindly provided by S.V. Zagrebelny. The second sample was collected from a calf stranded on Severo-Zapadnoye ("North-Western") rookery on Bering Island on September 28, 2011. This sample was kindly provided by E.G. Mamaev.

All samples were stored in 70 or 96% ethanol.

Genetic Analysis

Genetic analysis was performed in the Molecular Diagnostic Center of the Severtsov Institute of Ecology and Evolution, RAS. The samples were ground using the mixer mill Retsch MM400.

DNA was extracted using KingFisher Flex Magnetic Particle Processor (Thermo Scientific) and InviMag Tissue DNA Kit (STRATEC Molecular, Germany) according to the manufacturer's manual. DNA solution was stored at –20°C. We defined the allelic composition of nine microsatellite loci of nuclear DNA: 464/465 (for the sequences of primers see Fullard et al., 2000), DlrFCB12, DlrFCB13, DlrFCB17 (Buchanan et al., 1996), MK5, MK9 (Krutzen et al., 2001), Ttr11, Ttr48 (Rosel et al., 2005), Dde66 (Coughlan et al., 2006). One of the primers in each pair was labeled with a fluorescent dye (FAM, R6G, ROX or TAMRA). Amplification of the selected regions was performed using Mag Mix 2025 PCR master mix (Dialat Ltd., Russia). All primers were synthesized by JSC Syntol (Russia).

Fragment analysis was performed with AB3130 analyzer in presence of GeneScan 500 LIZ Size Standard (Applied Biosystems). To decode the signal, we used the software Gene Mapper v. 4.1 (Applied Biosystems).

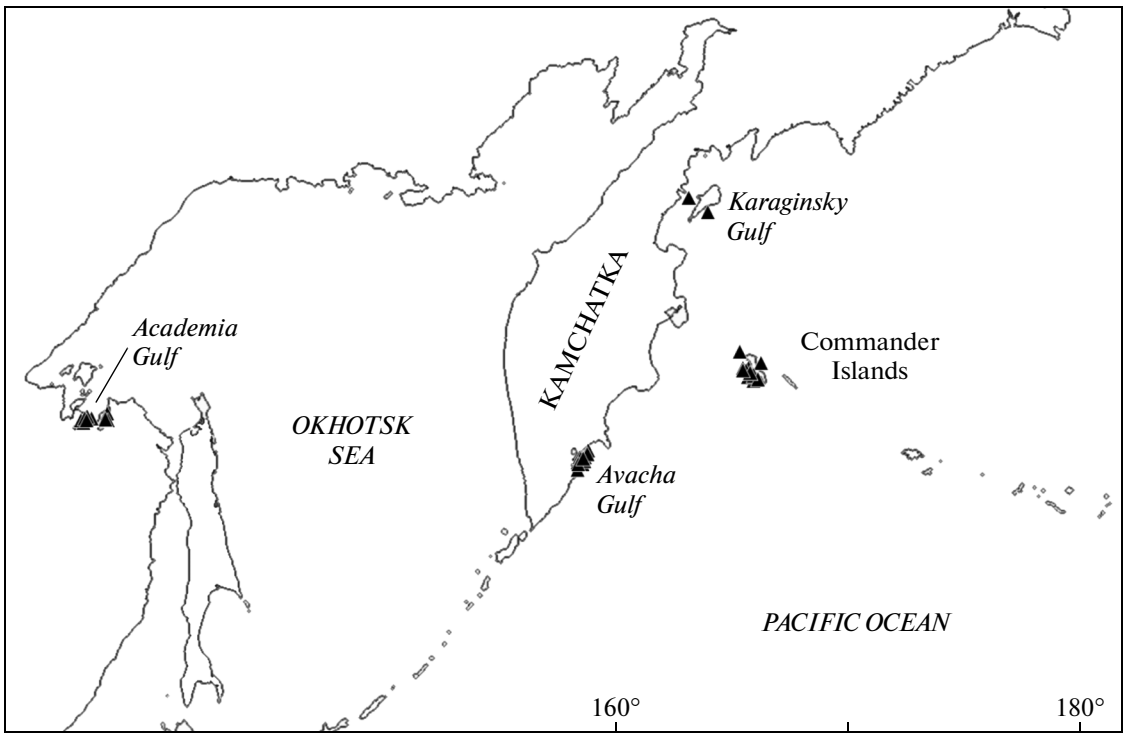

Fig. 1. Map of Russian Far Eastern seas showing the regions where the samples were collected. Locations of sample collection points are shown in black triangles.

The probability of individuals belonging to one or more possible reproductive groups was estimated using the clustering algorithms implemented in STRUCTURE v. 2.3.3 (Pritchard et al., 2000). In the "admixture" model, each individual is allowed to have partial ancestry in each of the K clusters; "admixture-LOCPRIOR" model uses the sampling location as default information to assist clustering. A logarithm of probability (ln Pr(X|K)) was estimated for different values of K (the prospective number of populations) as an average of three sequential estimates based on 500000 replicas each. The highest value of this logarithm indicates the maximum probability of the existence of the corresponding number of populations (genetic groups). To define the degree of genetic differentiation between the putative populations in the frequencies of different alleles (F_{st} index) and the level of its statistical significance we used the algorithm implemented in Arlequin v. 3.11 (Excoffier et al., 2005).

Isotope Analysis

Nitrogen isotope composition ($^{15}N/^{14}N$ ratio) was determined in the Mass-spectrometer collective usage center in the Severtsov Institute of Ecology and Evolution RAS. Samples were dried at 50°C for 48 h. Then we ground the dried samples to a powder, and aliquots of 500–600 μg were sealed in tin capsules. Isotope composition was determined using a Thermo-Finnegan Delta V Plus Mass Spectrometer coupled to a Flash 1112 Elemental Analyzer. Measurement errors did not exceed ±0.20‰.

We report stable isotope ratios as per mille (‰) using delta notation determined from the equation: $\delta^{15}N = ((R_{sample}-R_{standard})/R_{standard}) \times 1000$, where R_{sample} is the ratio of $^{15}N/^{14}N$ in the sample, and $R_{standard}$—the same ratio in the international standard (atmospheric N_2).

As a result of fractioning of heavy isotope in the consumer's organism, each trophic level is enriched compared to the lower one. For nitrogen, differences between the adjacent trophic levels typically comprise 2–3‰ (McCutchan et al., 2003; Michener and Kaufman, 2008).

For some samples it was not possible to run isotope analysis, because it requires the larger piece of skin than DNA extraction. We used 25 samples from Avacha Gulf, 2 samples from Karaginsky Gulf, 11 samples from the Commander Islands and 8 samples from the western Okhotsk Sea for isotope analysis.

Analysis of Saddle Patch Shape

For all sampled killer whales (except the stranded ones) the photographs of the saddle patch were obtained. Only photos of the left-side were used for the analysis, which is commonly accepted for killer whale photoidentification (Bigg et al., 1990). Saddle patch of

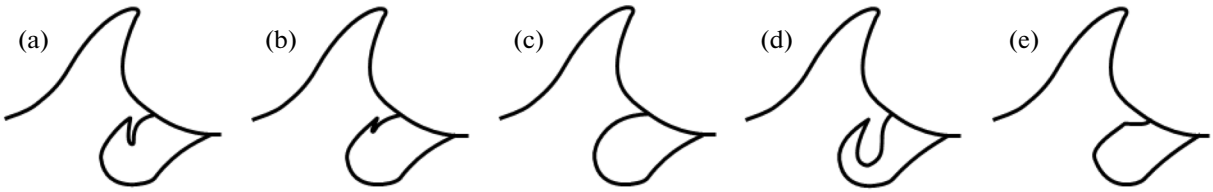

Fig. 2. Types of saddle patch shape (from Baird, Stacey, 1988): (a) medium notch, (b) small notch, (c) smooth, (d) large notch, (e) dimple.

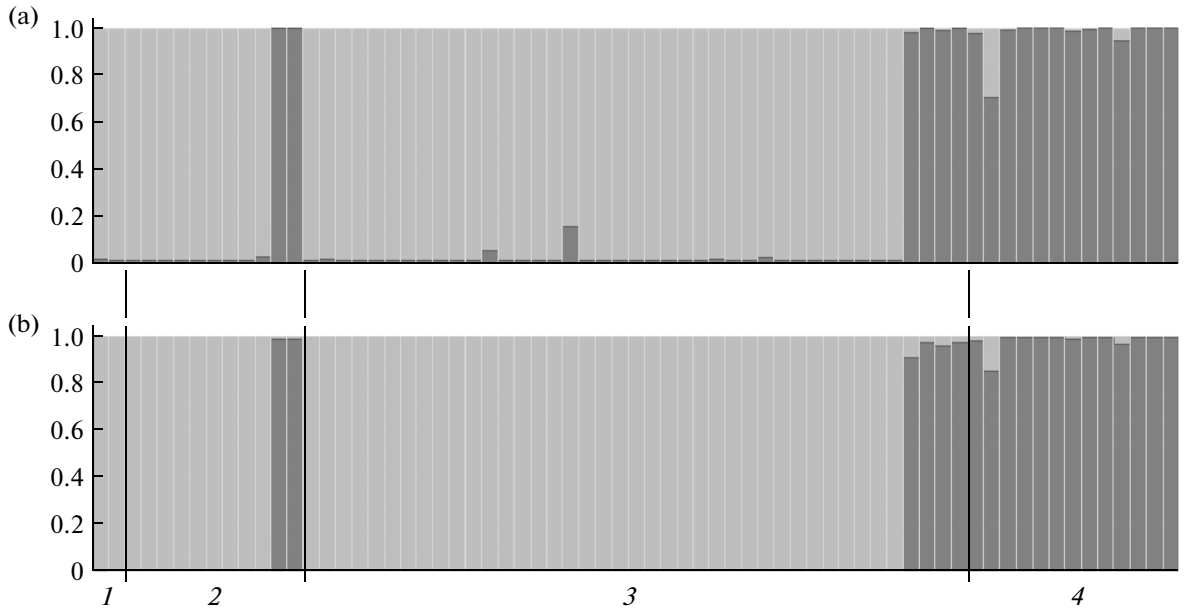

Fig. 3. STRUCTURE clustering results for K = 2. Each individual is represented by a single vertical bar, with estimated membership in each cluster denoted by the different colors. (a) "admixture" model, (b) "admixture-LOCPRIOR" model that considers the locations of sampling points. *1*—Karaginsky Gulf, *2*—Commander Islands, *3*—Avacha Gulf, *4*—Academia Gulf.

each individual was categorized into one of five types according to Baird and Stacey (1988) (Fig. 2). Then we compared the frequencies of occurrence of different types of saddle patch in two clusters revealed by genetic analysis.

RESULTS

Genetic Analysis

Analysis of the individual genotypes using "admixture" model shows a clear division of the studied animals into two genetic clusters (Fig. 3a): average value of lnPr was −1231.4 for K = 2 vs. −1451.0 for K = 1. The similar result was obtained with "admixture-LOCPRIOR" model that uses the information about sampling locations: the samples were assigned to one of the two clusters irrespective of the sampling location (Fig. 3b). The first cluster included both samples from Karaginsky Gulf, nine samples from Commander Islands and 37 samples from Avacha Gulf, the second cluster—two samples from Commander Islands, four samples from Avacha Gulf and all 13 samples from the western Okhotsk Sea. Maximum value of lnPr (−1217.9) while testing four geographical groups was reached at K = 2, while at K = 1, K = 3 and K = 4 the values were smaller: −1450.9, −1225.2 and −1243.1, respectively.

Occurrence of alleles between these two clusters differed significantly: $F_{st} = 0.23277$ ($p < 0.00001$), indicating reproductive isolation. The clusters differed not only in the allele frequencies, but also in the presence of unique alleles. The first cluster had unique alleles in 4 of 9 studied loci, their cumulative share of the total number of alleles was 11.3%, and total frequency 17.4%. The second cluster had unique alleles in all 9 loci, their share was 47.2%, and total frequency 34.5%.

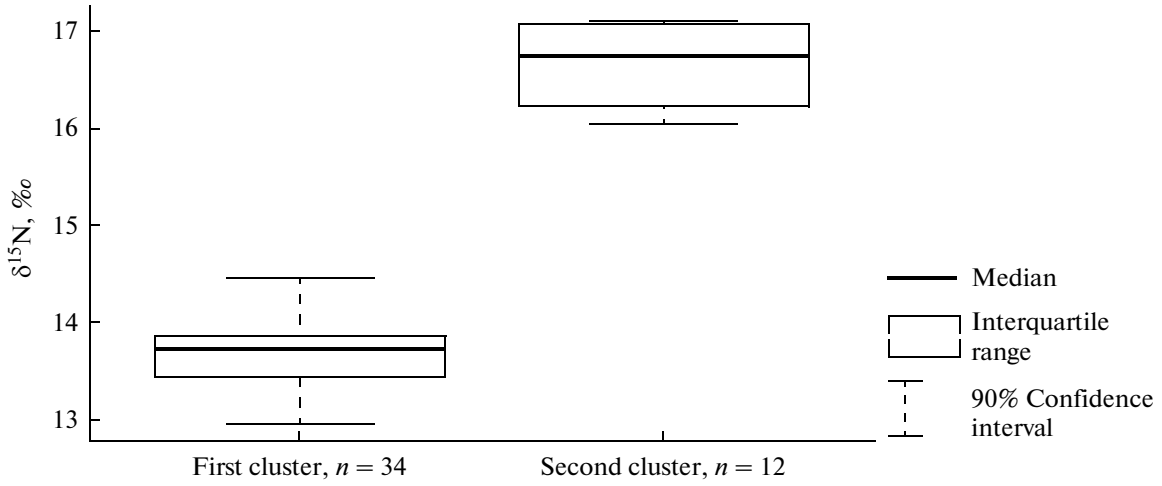

Fig. 4. Values of $\delta^{15}N$ in the samples from the first and the second genetic clusters.

Isotope Analysis

We compared $\delta^{15}N$ values in the samples from the animals assigned to the first and the second clusters by genetic analysis. $\delta^{15}N$ values were much lower in the first, when compared to the second, cluster: median ± standard deviation was 13.7 ± 0.4 and 16.8 ± 0.8‰, respectively. The difference between clusters was statistically significant (Mann-Whitney test, $n_1 = 34$, $n_2 = 12$, $U = 0$, $p < 0.0001$).

The observed difference between clusters, roughly 3‰, approximately corresponds to the difference between the adjacent trophic levels, i.e. the killer whales from the second cluster were about one trophic level above the killer whales from the first cluster.

Analysis of Saddle Patch Shape

Types of saddle patch shape occurred with different frequency in two genetic clusters. In the first cluster, all five types of saddle patch shape described for the northeastern Pacific fish-eating killer whales were found in different proportions: 6 killer whales had type "a" saddle patch, 6 whales had type "b" patch, 18 whales had type "c" patch, 2 whales had type "d" patch and 16 had type "e" patch. In the second cluster, only type "c" patches were found. Difference in the frequency of occurrence of saddle patch types across two genetic clusters was statistically significant (Fisher test, $p < 0.001$).

DISCUSSION

Our results demonstrate that killer whales in the Russian Far Eastern seas are divided into at least two reproductively isolated clusters that have stable ecological and morphological differences. Genetic analysis assigned the majority of samples from Avacha Gulf and Commander Islands and both samples from Karaginsky Gulf to the first cluster. The rest of the samples from Avacha Gulf and Commander Islands and all samples from the western Okhotsk Sea were assigned to another cluster that was significantly different from the first one in allele frequencies. Difference between clusters was high enough to suggest their reproductive isolation.

The content of heavy nitrogen (^{15}N) was significantly higher in the samples from the second than from the first genetic cluster, suggesting the higher trophic level for the whales from the second cluster (Michener and Kaufman, 2008). Apparently, the first cluster is represented by fish-eating, and the second—by mammal-eating killer whales described previously in Russian waters (Burdin et al., 2004).

The diet of fish-eating killer whales in Avacha Gulf mostly consists of various salmon species (*Oncorhynchus* sp.) and Atka mackerel (*Pleurogrammus monopterygius*) (Nagaylik, 2011). We have never observed fish-eating killer whales attacking other marine mammals, which are often encountered in the area. In Karaginsky Gulf, one of the sampled groups demonstrated behavior that suggested feeding on fish (our unpublished data), but we were unable to determine the prey species. In the Commander Islands, killer whales can feed on cod (*Gadus macrocephalus*) (Marakov, 1967), coho salmon (*Oncorhynchus kisutch*) (our unpublished data) and other salmon species.

As for mammal-eating killer whales, the individuals that look like them are rare in Avacha Gulf, but once we have occasionally observed them feeding on minke whale (Filatova et al., 2013). In the Commander Islands, attacks on Northern fur seals (*Callorhinus ursinus*) near rookeries are regularly observed (Mamaev and Burkanov, 2006; Belonovich et al., 2012), and in July 2013 we have observed a successful attack on Dall's porpoise (*Phocoenoides dalli*) (our unpublished data). In the coastal waters of the western Okhotsk Sea, killer whale hunts on bearded seal (*Eri-*

gnathus barbatus) and bowhead whale (*Balaena mysticetus*) were described (Shpak, 2012).

Intra-species divergence of foraging specialization has been described for many animals. Usually such divergence arise on an individual (e.g., Bryan and Larkin,1972; Thiemann et al., 2011) or group (Carmichael et al., 2001) level, but in the Pacific killer whales distinctive foraging specializations occur on population level. It is likely caused by the fact that for feeding on fish vs. marine mammals different behavioral adaptations are beneficial. For example, fish-eating killer whales are often highly vocal, while mammal-eating ones are usually silent, because their mammalian prey species have superior hearing and cognitive abilities allowing them detecting the predator by its sounds (Deecke et al., 2005). Another example is social structure: mean group size in mammal-eating killer whales is much smaller, than in fish-eating ones (Morton, 1990), because a smaller group has more chances, for example, to approach a seal haul-out unnoticed. On the contrary, fish-eating killer whales benefit from a larger group size: they spread over a wide area to search for a fish school, and when found it provides enough food for everyone. Difference in group size is achieved through variation in social structure: in fish-eating killer whales, both sexes remain in the natal family for their entire lives, while in mammal-eaters some whales can leave their family when reach maturity, joining other groups or forming new ones (Ford, 2002).

Phenetic differences in our sample set were similar to those described for killer whales from the Pacific coast of North America. Baird and Stacey (1988) showed that fish-eating killer whales from the Pacific Canada and Alaska had all five types of saddle patches, though type "c" patches were the most common. We also found all five saddle patch types in killer whales from the first cluster. The proportion of type "c" patches was slightly lower, and type "e" patches—slightly higher than in the North American conspecifics. In mammal-eating killer whales from Canada and Alaska type "c" patches prevailed and type "e" patches sometimes occurred. We have found only type "c" patches in the second cluster, which could be due to the small sample size. The presence of the stable phenetic differences further supports the reproductive isolation between clusters.

Interbreeding between fish-eating and mammal-eating whales has not been observed in the wild (Barrett-Lennard, 2000). There were no attempts to interbreed them in captivity, but both ecotypes successfully interbred with North Atlantic killer whales (captured off Iceland) and produced fertile offspring. Apparently, the degree of genetic differentiation between fish-eating and mammal-eating killer whales is too low to provide reproductive isolation on genetic level. Genetic differentiation in the wild is maintained because groups of fish-eating and mammal-eating killer whales never interact socially; when they meet they ignore or avoid each other (Ford, 2002). Therefore, behavioral rather than genetic reproductive isolation is more likely.

It has been repeatedly suggested to divide fish-eating and mammal-eating killer whales from the Pacific North America into two species (Baird et al., 1992; Reeves et al., 2004; Morin et al., 2010). However, it has not been done yet, likely because they are sympatric and similar in appearance, which makes them hard to identify at sea by inexperienced observers. However, sibling species have been described in many animals—from insects (fruit flies, Coyne, 1976) to birds (Avise and Zink, 1988) and mammals (voles, Malygin, 1983; bats, Arlettaz, 1999; African murid rodents, Volobouev et al., 2002). The lack of genetic reproductive isolation between ecotypes is also a problem, because such isolation is considered a key feature in the biological species concept (Mayr, 1942). Nevertheless, the ability to produce fertile interspecies hybrids has been described for many species (e.g., for European mink and polecat (*Mustela lutreola* × *M. putorius*) Tumanov and Abramov, 2002; bottlenosed and common dolphins (*Tursiops truncatus* × *Delphinus capensis*) Zornetzer and Duffield, 2003; harbor and Dall's porpoises (*Phocoena phocoena* × *Ph. dalli*) Willis et al., 2004), and it should not be considered a ponderable argument against the division of fish-eating and mammal-eating killer whales into separate species. Genus *Tursiops*, previously considered monotypic and being in a somehow similar situation, has recently been divided into three species: the common bottlenose dolphin (*T. truncatus*), the Indo-Pacific bottlenose dolphin (*T. aduncus*) and the Burrunan dolphin (*T. australis*) (Wells and Scott, 2002; Charlton-Robb et al., 2011).

The stable genetic, ecological and phenotypic differences between the killer whale groups in Russian waters unambiguously indicate that they are not just separate populations, but separate ecotypes, and maybe, considering the arguments listed above, separate species.

The results of our study of the killer whale populations in Russian waters are very important from the practical point of view. It is now obvious that fish-eating and mammal-eating killer whales must be considered separately for abundance surveys, monitoring, evaluation of human impact and estimates of total allowed takes from the wild populations. The current approach, when all killer whales within a certain area are considered a single management unit, is inadmissible, because it does not consider the biological characteristics of these animals. For the sustainable management, more studies are needed using the modern research methods (photoidentification, satellite tagging, genetic analysis) to define the distribution and size of killer whale populations of both ecotypes in the Russian waters.

ACKNOWLEDGMENTS

The samples from Avacha Gulf, Karaginsky Gulf and from the waters of the Commander Islands were collected as a part of the Far East Russia Orca Project. The samples from the western Okhotsk Sea were collected as a part of the project "Current Status of the Amur Stock Belugas (Sea of Okhotsk, Russia): Sustainability Assessment". We are grateful to all our colleagues who participated in the sampling: A.E. Volkov, A.M. Goskov, E.L. Dzhikiya, S.V. Zagrebelny, E.M. Lazareva, E.M. Mamaev, M.M. Nagaylik, A.Yu. Paramonov. We are grateful to T.V. Ivkovich who provided the photographs of sampled killer whales.

This work was funded by the Russian Fund for the Fundamental Research (grant no. 11-04-00460-a) and the Rufford Small Grants Foundation.

REFERENCES

Arlettaz, R., Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii, J. Anim. Ecol.*, 1999, vol. 68, pp. 460–471.

Avise, J.C. and Zink, R.M., Molecular genetic divergence between avian sibling species: King and Clapper Rails, Long-billed and Short-billed Dowitchers, Boat-tailed and Great-tailed Grackles, and Tufted and Black-crested Titmice, *Auk*, 1988, pp. 516–528.

Baird, R.W. and Stacey, P.J., Variation in saddle patch pigmentation in populations of killer whales (*Orcinus orca*) from British Columbia, Alaska, and Washington State, *Can. J. Zool.*, 1988, vol. 66, pp. 2582–2585.

Baird, R.W., Abrams, P.A., and Dill, L.M., Possible indirect interactions between transient and resident killer whales: implications for the evolution of foraging specializations in the genus *Orcinus, Oecologia*, 1992, vol. 89, pp. 125–132.

Barrett-Lennard, L.G., Population structure and mating patterns of killer whales, *Orcinus orca*, as revealed by DNA analysis, *Ph.D. Thesis*, Vancouver: Univ. of British Columbia, 2000.

Belonovich, O.A., Fomin, S.V., and Ryazanov, S.D., Transient killer whales off the Commander Islands, in *Materialy Kruglogo stola po kosatke, VII Mezhd. konf. "Morskie mlekopitayushchie Golarktiki"* (VII Int. Conf. "Marine Mammals of the Holarctic," Proc. Roundtable Debate on Killer Whale), 2012, pp. 15–17.

Bigg, M.A., Olesiuk, P.F., Ellis, C.M., Ford, J.K.B., and Balcomb, K.C., Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State, *Report of the International Whaling Commission Special Issue 12*, 1990, pp. 383–405.

Bryan, J.E. and Larkin, P.A., Food specialization by individual trout, *J. Fisher. Res. Board Canada*, 1972, vol. 29, pp. 1615–1624.

Buchanan, F.C., Friesen, M.K., Littlejohn, R.P., and Clayton, J.W., Microsatellites from the beluga whale, *Delphinapterus leucas, Mol. Ecol.*, 1996, vol. 5, pp. 571–575.

Burdin, A.M., Barrett-Lennard, L., Sato, H., and Hoyt, E., Preliminary results of studies on the genetics of killer whale (*Orcinus orca*) in the far eastern seas of Russia, in *Materialy Tret'ei mezhdunarodnoi konferentsii "Morskie Mlekopitayushchie Golarktiki"* (Proc. Third Int. Conf. "Marine Mammals of the Holarctic"), Koktebel, 2004, pp. 109–110.

Burdin, A.M., Hoyt, E., Sato, H., Tarasyan, K., and Filatova, O.A., Resident and Transient-type Killer Whales, *Orcinus orca*, in Southeast Kamchatka, Russia, IWC Scientific Committee, 2004 (SC/56/SM15).

Carmichael, L.E., Nagy, J.A., Larter, N.C., and Strobeck, C., Prey specialization may influence patterns of gene flow in wolves of the Canadian northwest, *Mol. Ecol.*, 2001, vol. 10, pp. 2787–2798.

Charlton-Robb, K., Gershwin, L., Thompson, R., Austin, J., Owen, K., and McKechnie, S., A new dolphin species, the Burrunan dolphin *Tursiops australis* sp. nov., endemic to southern Australian coastal waters, *PLoS One*, 2011, vol. 6, no. 9. e24047.

Coughlan, J., Mirimin, L., Dillane, E., Rogan, E., and Cross, T.F., Isolation and characterization of novel microsatellite loci for the short-beaked common dolphin (*Delphinus delphis*) and cross amplification in other cetacean species, *Mol. Ecol.*, 2006, vol. 6, pp. 490–492.

Coyne, J.A., Lack of genic similarity between two sibling species of *Drosophila* as revealed by varied techniques, *Genetics*, 1976, vol. 84, pp. 593–607.

Deecke, V.B., Ford, J.K.B., and Slater, P.J.B., The vocal behaviour of mammal-eating killer whales (*Orcinus orca*): communicating with costly calls, *Anim. Behav.*, 2005, vol. 69, pp. 395–405.

Excoffier, L., Laval, G., and Schneider, S., Arlequin v. 3.0: an integrated software package for population genetics data analysis, *Evol. Bioinform. Online*, 2005, vol. 1, pp. 47–50.

Filatova, O.A., Ivkovich, T.V., Shpak, O.V., Borisova, E.A., and Fedutin, I.D., Killer whales: fishers and hunters, *Priroda* (Moscow), 2013, no. 5, pp. 28–37.

Ford, J.K.B., Killer whales, in *The Encyclopedia of Marine Mammals*, New York: Academic, 2002, pp. 669–676.

Ford, J.K.B., Ellis, G.M., Barrett-Lennard, L.G., Morton, A.B., Palm, R.S., and Balcomb, K.C., Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters, *Can. J. Zool.*, 1998, vol. 76, pp. 1456–1471.

Ford, J.K.B., Ellis, G.M., Matkin, C.O., Wetklo, M.H., Barrett-Lennard, L.G., and Withler, R.E., Shark predation and tooth wear in a population of northeastern pacific killer whales (*Orcinus orca*), *Aquat. Biol.*, 2011, vol. 11, pp. 213–224.

Fullard, K.J., Early, G., Heide-Jørgensen, M.P., Loch, D., Rosing-Asvid, A., and Amos W., Population structure of long-finned pilot whales in the North Alantic: a correlation with sea surface temperature?, *Mol. Ecol.*, 2000, vol. 9, pp. 949–958.

Hoelzel, A.R. and Dover, G.A., Genetic differentiation between sympatric killer whale populations, *Heredity*, 1991, vol. 66, pp. 191–195.

Ivkovich, T.V., Filatova, O.A., Burdin, A.M., Sato, H., and Hoyt, E., The social organization of resident-type killer whales (*Orcinus orca*) in Avacha Gulf, Northwest Pacific, as revealed through association patterns and acoustic similarity, *Mammal. Biol.*, 2010, vol. 75, pp. 198–210.

Krahn, M.M., Ford, M.J., Perrin, W.F., Wade, P.R., Angliss, R.P., et al., *2004 Status Review of Southern Resident Killer Whales (Orcinus orca) under the Endangered Species*

Act, NOAA Tech. Memo NMFSNWFSC-62, U.S. Dept. Commerce, 2004.

Krutzen, M., Valsecchi, E., Connor, R.C., and Sherwin, W.B., Characterization of microsatellite loci in *Tursiops aduncus, Mol. Ecol.*, 2001, vol. 1, pp. 170–172.

Malygin, V.M., *Sistematika obyknovennykh polevok* (Taxonomy of Common Voles), Moscow: Nauka, 1983.

Mamaev, E.G. and Burkanov, V.N., Killer whales (*Orcinus orca*) and northern fur seals (*Callorhinus ursinus*) of the Commander Islands: formation of food specialization?, in *Sbornik nauchnykh trudov po materialam shestoi mezhdunarodnoi konferentsii Morskie mlekopitayushchie Golarktiki* (Collected Scientific Papers Based on Materials of the Sixth International Conference "Marine Mammals of the Holarctic"), 2006, pp. 347–351.

Marakov, S.V., Cetaceans in the waters off the Commander Islands, *Tr. Polyar. Inform.-Issled. Proekt. Inst. Morsk. Ryb. Khoz. Okeanogr.*, 1967, no. 21, pp. 200–210.

Mayr, E., *Systematics and the Origin of Species from the Viewpoint of a Zoologist*, New York: Columbia Univ. Press, 1942.

McCutchan, J.H., Lewis, W.M., Kendall, C., and McGrath, C.C., Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur, *Oikos*, 2003, vol. 102, pp. 378–390.

Michener, R.H. and Kaufman, L., Stable isotope ratios as tracers in marine food webs: an update, in *Stable Isotopes in Ecology and Environmental Science*, 2nd ed., Oxford, UK: Blackwell, 2008, pp. 238–278.

Morin, P.A., Archer, F.I., Foote, A.D., Vilstrup, J., Allen, E.E., et al., Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species, *Genome Res.*, 2010, vol. 20, pp. 908–916.

Morton, A.B., A quantitative comparison of the behavior of resident and transient forms of the killer whale off the central British Columbia coast, *Report of the International Whaling Commission Special Issue 12*, 1990, pp. 245–248.

Nagaylik, M.M., Spatial population structure and behavior of killer whales off eastern Kamchatka, *Cand. Sci. (Biol.) Dissertation*, Moscow: Moscow State Univ., 2011.

Pitman, R.L. and Ensor, P., Three forms of killer whales (*Orcinus orca*) in Antarctic waters, *J. Cetacean Res. Manag.*, 2003, vol. 5, pp. 131–140.

Pitman, R.L., Durban, J.W., Greenfelder, M., Guinet, C., Jorgensen, M., et al., Observations of a distinctive morphotype of killer whale (*Orcinus orca*), type D, from subantarctic waters, *Polar Biol.*, 2010, vol. 34, pp. 303–306.

Pritchard, J.K., Stephens, M., and Donnelly, P., Inference of population structure using multilocus genotype data, *Genetics*, 2000, vol. 155, pp. 945–959.

Reeves, R.R., Perrin, W.F., Taylor, B.L., Baker, C.S., and Mesnick, S.L., Report of the workshop on shortcomings of cetacean taxonomy in relation to needs of conservation and management, La Jolla, California, *NOAA Technical Memorandum NMFS-SWFSC*, vol. 363, 2004.

Rosel, P.E., Forgetta, V., and Dewar, K., Isolation and characterization of twelve polymorphic microsatellite markers in bottlenose dolphins (*Tursiops truncatus*), *Mol. Ecol.*, 2005, vol. 5, pp. 830–833.

Saulitis, E.L., Matkin, C.O., Barrett-Lennard, L.G., Heise, K., and Ellis, G.M., Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska, *Mar. Mammal Sci.*, 2000, vol. 16, pp. 94–109.

Shpak, O.V., Carnivorous killer whales (*Orcinus orca*) in the western Sea of Okhotsk: observations and questionnaire data, in *Materialy kruglogo stola po kosatke, VII Mezhd. konf. "Morskie mlekopitayushchie Golarktiki"* (VII Int. Conf. "Marine Mammals of the Holarctic," Proc. Roundtable Debate on Killer Whale), 2012, pp. 17–21.

Thiemann, G.W., Iverson, S.J., Stirling, I., and Obbard, M.E., Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore, *Oikos*, 2011, vol. 120, pp. 1469–1478.

Tumanov, I.L. and Abramov, A.V., A study of the hybrids between the European mink *Mustela lutreola* and the polecat *M. putorius, Small Carnivore Conserv.*, 2002, vol. 27, pp. 29–31.

Volobouev, V.T., Aniskin, V.M., Lecompte, E., and Ducroz, J.-F., Patterns of karyotype evolution in complexes of sibling species within three genera of African murid rodents inferred from the comparison of cytogenetic and molecular data, *Cytogenet. Genome Res.*, 2002, vol. 96, pp. 261–275.

Wells, R. and Scott, M., Bottlenose dolphins, in *Encyclopedia of Marine Mammals*, New York: Academic, 2002, pp. 122–127.

Willis, P.M., Crespi, B.J., Dill, L.M., Baird, R.W., and Hanson, M.B., Natural hybridization between Dall's porpoises (*Phocoenoides dalli*) and harbour porpoises (*Phocoena phocoena*), *Can. J. Zool.*, 2004, vol. 81, pp. 828–834.

Zornetzer, H.R. and Duffield, D.A., Captive-born bottlenose dolphin × common dolphin (*Tursiops truncatus* × *Delphinus capensis*) intergeneric hybrids, *Can. J. Zool.*, 2003, vol. 81, pp. 1755–1762.