EVOLUTION

Species IN THE Making

Killer whales appear to be splitting into several separate species, perhaps because cultural differences among populations are driving them apart

By Rüdiger Riesch

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JUST OFFSHORE FROM THE PEBBLE BEACHES OF BERE POINT ON MALCOLM ISLAND, British Columbia, the *Naiad Explorer* rocks gently in the waters of the Queen Charlotte Strait. The sun has burned off most of the morning mist, save for a thin layer that still shrouds the tips of the island's cedars, firs and spruces. I watch from the boat as three killer whale brothers named Cracroft, Plumper and Kaikash gently scrape their bodies against the small, smooth stones in the shallows off the bow. The brothers have already spent the better part of an hour here absorbed in this activity. Soon they will leave to hunt for salmon or look for mates.

Exactly why the creatures engage in this scraping behavior, known as beach rubbing, is uncertain. Most experts assume that it aids in sloughing off dead skin and dislodging external parasites, but it might also be for pleasure. Whatever the motivation behind it, beach rubbing, though rarely observed in other cetaceans—the group that includes whales, dolphins and porpoises—is commonplace here. It is part of the distinctive cultural fabric of the northern resident killer whales, a community that claims the waters around northern Vancouver Island as home during the summer months. (Despite their name, killer whales are actually large dolphins.)

The northern resident killer whales are not the only ones with unique behaviors. Observations made since the 1970s have shown that killer whale populations around the globe each have unique ways of doing everything from hunting to communicating. Physical traits, including coloration, body size and dorsal fin shape, vary among groups as well, albeit somewhat more modestly. These cultural and physical differences, along with the astonishing degree of genetic diversity documented in these creatures over the past 15 or so years, suggest to me and many other researchers that today's killer whale populations, rather than simply representing the single species scientists have long envisioned, are actually in the midst of going their separate evolutionary ways. That is, they appear to be splitting into new species that, if this process continues, ultimately will be unable to produce viable or fertile offspring with one another.

Intriguingly, their cultural differences may be driving this diversification: the whales seem to mate with individuals that largely share their customs, to the exclusion of those that do not, a preference that creates the conditions needed for speciation to occur. If so, then killer whales could provide a striking example of a speciation mechanism not considered in the classical theory of how new species arise. They might also offer insights into how another group of creatures—*Homo sapiens* and our extinct predecessors—diverged into an array of species that once shared the planet.

A DIVERSITY OF KILLERS

FOR MORE THAN A CENTURY biologists have looked to geography to explain how speciation occurs. In the favored scenario, called allopatric speciation, two populations of an ancestral species

IN BRIEF

Evolutionary biologists have long turned to geography to explain the emergence of new species.
In the classic explanation, two populations of an ancestral species become separated by a geographical barrier that prevents them from interbreeding, thereby allowing each group to follow its own evolutionary trajectory.
Killer whale populations appear to be going separate evolutionary pathways despite the fact that no known geographical barriers separate them.
Mounting evidence indicates that cultural differences related to food acquisition are driving these populations apart.
The killer whale findings raise questions about diversification within another culture-bearing group of organisms: members of the human family.

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become physically separated from each other, often by a geographical barrier of some kind—perhaps a mountain range, desert or river—that prevents the populations from interbreeding. If this separation persists long enough, over time each population will follow its own independent evolutionary trajectory, acquiring different genes that may help them survive in different environmental conditions, for example, or that may accumulate randomly through a process known as genetic drift. Eventually, so the theory goes, the two populations can become so genetically different from each other that if they come into contact again, they cannot interbreed successfully.

Overwhelming evidence from numerous organisms ranging from species of *Alpheus* snapping shrimp that live on either side of the Isthmus of Panama to *Cyprinodon* pupfish species found only in isolated springs in California and Nevada shows that geographical isolation does indeed facilitate the speciation process. Yet sometimes two or more subpopulations of dissimilar appearance will emerge within the same geographical area and ultimately differentiate into separate species. Scientists, including famed German evolutionary biologist Ernst Mayr, traditionally held that at least some period of isolation was essential to the process of speciation and that speciation entirely within the same area was therefore either impossible or at least very rare. More recent work has demonstrated that geographical isolation in the traditional sense is not always necessary for speciation to occur, however.

Indeed, biologists now largely accept that certain species, among them the astonishingly diverse cichlid fishes found in the crater lakes of East Africa and Nicaragua, as well as the *Howea* palm trees found on Lord Howe Island in the Pacific, have evolved in the absence of such isolation. In the parlance of biologists, they have undergone sympatric speciation, and in the case of cichlids, this was apparently mostly driven by different cichlids adapting to exploit different food sources (but without the influence of culture), whereas different Lord Howe palms have evolved different flowering times. Documented examples of sympatric speciation among mammals are rare, though, which makes the case of the killer whales especially interesting.

Killer whales (also called orcas and, in some regions, blackfish) are the most widely distributed mammal on earth after humans. They inhabit all the world's oceans and can travel more than 100 kilometers a day or upward of several thousand kilometers within just a few weeks. There are no known geographical barriers that would prevent individuals from one population from mingling with members of neighboring populations. Yet scientists have now shown that in various marine areas, several ecologically distinct forms, or ecotypes, of killer whales live side by side without fraternizing. One type, for instance, might live mainly on a particular kind of fish, whereas another type might prefer seals.

The best-studied assemblage of killer whale ecotypes lives in the Northeast Pacific. There research begun in the early 1970s by Canadian scientist Michael Bigg led to many remarkable discoveries. First, he noticed that individual killer whales differed in the shape and size of their dorsal fins and in the shape, size and coloration of the so-called saddle patch—the grayish white area behind the dorsal fin. Biologists can use those traits to identify individual killer whales, just as forensic scientists use facial features and fingerprints to identify individual humans. Second, Bigg and his colleagues, including John K. B. Ford and Graeme M. Ellis, both at Fisheries and Oceans Canada, and Kenneth C. Balcomb III of the Center for Whale Research in Washington State, found that three different killer whale ecotypes coexist in the waters off the West Coast of the U.S. and Canada: the so-called resident, transient and offshore forms. Resident killer whales specialize in foraging for fish, especially salmon; transient killer whales target marine mammals and the occasional seabird; and offshore killer whales seem to specialize in a second kind of fish diet that includes Pacific halibut and Pacific sleeper sharks, although their habits remain largely mysterious because encounters with them are rare.

In recent years research led by Olga A. Filatova of Moscow State University, Alexander M. Burdin of the Russian Academy of Sciences, and Erich Hoyt of Whale and Dolphin Conservation in England has revealed that residentlike and transientlike ecotypes also share the Russian waters of the Northwest Pacific around the Kamchatka Peninsula. Thus, we now know that there is a more or less continuous band of resident populations coexisting with transient populations that connect the Northeast Pacific with the Northwest Pacific via the Aleutian Islands.

Halfway across the world, killer whale populations from around Iceland, Shetland and Norway in the Northeast Atlantic have their own food preferences. Scientists, including Volker B. Deecke of the University of Cumbria in England, Andrew D. Foote of the University of Bern in Switzerland and their colleagues, have reported on two groups: type 1 killer whale populations forage for fish, in particular herring and mackerel, and type 2 killer whales pursue seals. More research is needed to fully understand the dietary differences between the groups.

The Southern Hemisphere hosts geographically overlapping ecotypes, too. John W. Durban and Robert L. Pitman, both at the National Oceanic and Atmospheric Administration, and their colleagues have discovered at least four different ones in Antarctic and sub-Antarctic waters. "Type A" killer whales appear to specialize in hunting Antarctic minke whales, "type B" killer whales, on the other hand, come in a large form (the so-called pack ice killer whale) that focuses on seals, and a small form (the Gerlache killer whale) that favors penguins. "Type C"—the smallest known killer whale—hunts Antarctic toothfish. For its part "type D," like the offshore killer whales of the North Pacific, seems to be an open ocean ecotype that remains largely elusive. This ecotype is known to eat Patagonian toothfish from longline fisheries, but it probably dines on other prey as well.

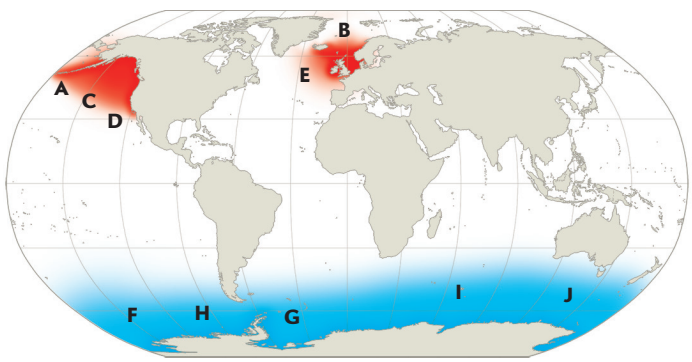
Once scientists realized that all these factions existed within the killer whales, they began to wonder about the origins of these groups. Were the populations already living in the same geographical region when they started to differentiate, or did they start diverging at a time when they lived apart and only later colonized the same region after they had already started down separate evolutionary paths? Current evidence is mostly inconclusive for many Northern Hemisphere killer whales. Whereas several studies by Foote and his colleagues suggest that killer whale divergence in the North Pacific happened while populations were geographically isolated (allopatric speciation), other analyses by Alan Rus Hoelzel of Durham University in England and his collaborators hint that these ecotypes might have always co-existed (sympatric speciation). For the killer whales of the Antarctic, though, the evidence is clearer:

A Resident
Preferred prey: fish, especially salmon

Kinds of Killers

Killer whales live in all the world's oceans, without any geographical barriers to keep their populations from interbreeding. Yet studies show that in various regions distinct forms, or ecotypes, have arisen despite living in close proximity to one another. These separate groups, which do not interbreed, differ in their prey choices and how they hunt. They also differ in their physical features, such as body size and coloration, eye patch size, and the shape of the dorsal fin and the saddle patch behind it. The whales choose mates that share their customs rather than foreigners from other ecotypes. Culture appears to keep the ecotypes apart, promoting speciation.

B Type 1
Preferred prey: herring and mackerel



F Type B (Pack Ice)
Preferred prey: seals

H Type A
Preferred prey: Minke whales

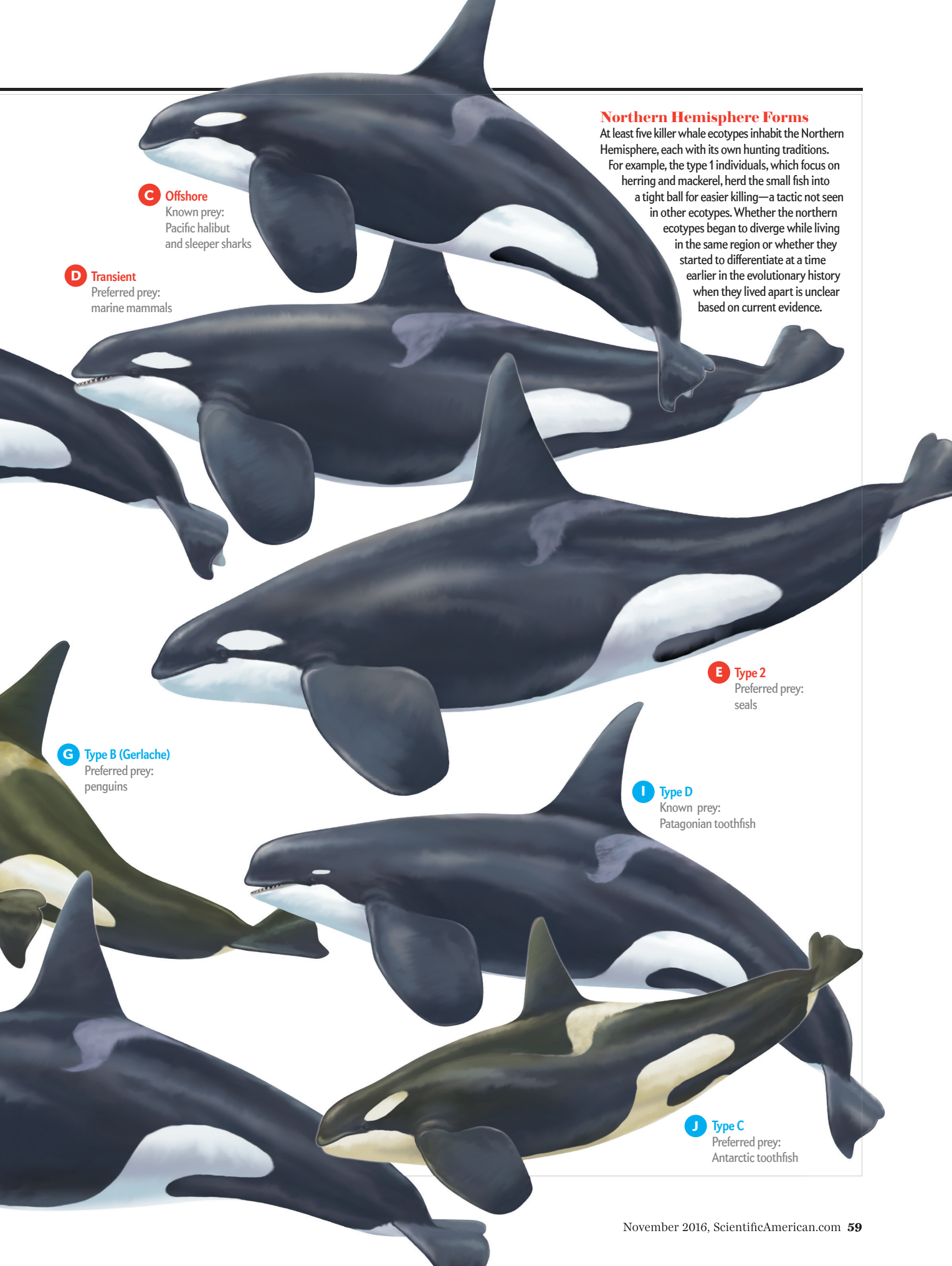
Southern Hemisphere Forms

The Antarctic and sub-Antarctic waters harbor at least five killer whale varieties. Their cultural traditions probably differ depending on their preferred prey. For instance, members of the type B pack ice ecotype have developed a unique strategy called wave washing to push seals off ice floats and into the water, where they are easier to nab. DNA studies indicate that the majority of these forms most likely diverged while living in the same geographical region.

Illustration by Amadeo Bachar

Northern Hemisphere Forms

At least five killer whale ecotypes inhabit the Northern Hemisphere, each with its own hunting traditions. For example, the type 1 individuals, which focus on herring and mackerel, herd the small fish into a tight ball for easier killing—a tactic not seen in other ecotypes. Whether the northern ecotypes began to diverge while living in the same region or whether they started to differentiate at a time earlier in the evolutionary history when they lived apart is unclear based on current evidence.



POD of killer whales surfaces off the coast of British Columbia.

HIROYA MINAKUCHI *National Geographic Creative*

most, if not all, of these killer whale ecotypes probably diverged sympatrically while living in the same geographical region.

However the now sympatric ecotypes initially began to diverge, they did so rapidly. In May of this year, Foote and his colleagues reported that their genomic analysis of five killer whale ecotypes from the North Pacific and the Antarctic showed that these forms evolved from a common ancestor within the past 250,000 years. What is keeping them separate now? Breeding records maintained and occasionally published by SeaWorld, which houses killer whales originally captured in both the North Atlantic and the North Pacific, demonstrate that matings between different killer whale ecotypes produce viable and fertile offspring, in contrast to the usually infertile mules and hinnies that result from hybridization between horses and donkeys. It is therefore extremely unlikely that genetic incompatibilities between killer whale ecotypes are preventing interbreeding in natural populations. Rather mounting evidence suggests that cultural differences are to blame.

CULTURE CLASH

LIKE MANY ORGANISMS that have undergone speciation, killer whales are diversifying by exploiting different food sources and evolving various traits that presumably help them get those foods. Some of these distinguishing features are physical, such as the generally larger, stronger build of the mammal-hunting killer whales. But the most dramatic specializations have occurred in cultural behaviors related to food acquisition. Because these and other behaviors are found only in certain populations where they appear to be passed on between members of the same generation and from generation to generation through social interactions (so-called social learning), rather than being innate, biologists consider them to be cultural.

For example, populations of killer whales that hunt marine mammals have learned to intentionally strand themselves to capture inexperienced sea lion and elephant seal pups right off the beach. Scientists have observed this behavior in two groups of killer whales that are distinct from the previously mentioned ecotypes. One inhabits the waters around the Crozet Archipelago in the Indian Ocean between Africa and Antarctica; the other dwells near the Peninsula Valdés on Argentina's Atlantic Coast. Apparently both populations invented this hunting strategy independently in response to their prey choices and the physical characteristics of their hunting grounds, where deep water channels and river outlets allow the killer whales to stay largely submerged until they are just meters away from their quarry.

In Antarctica, the large, pack ice form of the type B killer whales have invented another ingenious hunting strategy to gain access to seals: wave washing. The seals often haul out on small ice floats, where they feel safe from predators. But the ice-pack killer whales have learned to create waves that wash the seals over the ice float and into the water, where they are easier to nab.

Type 1, fish-eating killer whales around Iceland and Norway, for their part, have developed an entirely different strategy—dubbed carousel feeding—to hunt the herring that form the mainstay of their diet. A pod of the killer whales will herd a school of herring into a tight ball close to the water surface,

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where the fish cannot escape into the depths. Then individual pod members will swim right into the ball and slam their tail fins into the fish to debilitate and kill them.

Killer whales even communicate differently depending on what they eat. Indeed, it is in their acoustic communication signals that the most astonishing cultural diversity is found. Like other dolphins, they use three different acoustic signals: echolocation clicks, which are used to navigate and to locate prey, and pulsed calls and whistles, both of which are used for communication with their compatriots. Not only do the pulsed calls and whistles differ among killer whales from different geographical regions, but they also differ among populations that inhabit the same region.

The reason for this intraregional variation in signal production and use becomes clear when one considers the different challenges the ecotypes face. Killer whales that hunt marine mammals, for example, must contend with the excellent underwater hearing ability of their quarry: eavesdropping prey can use any sound the killer whales produce to detect them and subsequently evade capture. Transient killer whales in the Northeast Pacific and mammal-hunting killer whales in the North Atlantic thus use acoustic signals only very sparingly; most of the time they swim and hunt in stealth mode. Fish-eating killer whales do not have the same problem, so they are typically very chatty with one another, and they do not skimp on echolocation when navigating and tracking prey.

Furthermore, many pulsed calls and, as some of my own research has shown, some whistles are highly stereotyped. That is, the signals can be further differentiated into discrete sounds, like letters in an alphabet. (There is no evidence to suggest that killer whales use these signals in any way that really resembles our human use of words and sentences, however. Rather the context within which a signal is used seems to provide the meaning.) These discrete sounds exhibit geographical variation and ecotype variation. But they also often vary among social groups within an ecotype. For instance, among northern resident killer whales—a population of fish-eating killer whales that inhabits the waters from approximately around the middle of Vancouver Island up into southeastern Alaska—each family unit has its own repertoire of seven to 17 discrete calls. Killer whale families that share a portion of their dialects are grouped together into acoustical clans: A-clan, G-clan and R-clan for the northern resident killer whales.

The different discrete call types and family dialects are so distinctive that those of us who work on these killer whale populations can assign individuals into the correct ecotype, clan (for northern resident killer whales) or even family unit, based on recordings of their discrete call repertoire alone. These differences figure importantly in mate choice. Genetic analyses of the northern residents by Lance Barrett-Lennard of the Vancouver Aquarium Marine Science Center have shown that call similarity largely mirrors genetic similarity. Most matings take place between members of different clans, which have correspondingly different calls. The finding implies that northern residents find other northern residents that sound different from themselves more attractive than those that sound similar. Thus, the dialects offer a nifty way to prevent inbreeding.

That killer whales have all these ecotype-specific customs and appear to dislike socializing and mating with foreigners from other ecotypes despite being biologically capable of doing so suggests that culture is keeping these ecotypes apart. Eventually, if this separation persists for enough generations, then these different ecotypes might evolve additional differences in their DNA that could render them genetically incompatible. Culture in killer whales thus has the potential to take the place of geographical isolation in facilitating speciation by preventing mixing between populations.

The killer whale findings raise interesting questions about diversification within the human family. Traditionally anthropologists thought that most selective pressures that shaped our evolution were the result of changes happening purely in our external environment. But recent genetic analyses indicate that a large part of our evolution might have resulted from certain sometimes very locally restricted, cultural innovations. The practice of cattle farming has driven the evolution of lactose tolerance in certain European and African populations; the high-fat diet of Inuit people in Greenland has driven the evolution of a more efficient fat metabolism in that population. Although all modern human populations clearly belong to the same species and mix routinely with one another, for most of human prehistory, multiple human species shared the planet. Might culture have also played a role in driving speciation among those early members of the human family?

SEPARATE WAYS

DESPITE THE AMAZING ADVANCES in decoding how killer whales have diversified, scientists still have much to learn. Do other areas in less researched regions of the world also host sympatric killer whale ecotypes? Some preliminary studies hint that the oceans around Africa might; those around South America and southern Asia come to mind, too. Also, what are the communications systems of Antarctic and sub-Antarctic killer whales like, and what are their social structures? With the advent of modern tools for studying genomes, the future of speciation research in general—and killer whale research in particular—looks very bright. Perhaps in the not so distant future these and other new technologies will enable us to unequivocally determine what the geographical arrangements of killer whale populations were during all phases of their diversification.

Already we know that culture can divide killer whale populations that live side by side. Maybe a few years from now biologists will recognize these ecotypes as different species, each restricted to a certain geographical area of our oceans, each with its own very specific diet and customs, each with the potential to diverge and form yet more new twigs on the tree of life. SA

MORE TO EXPLORE

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FROM OUR ARCHIVES

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