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Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales?

Rüdiger Riesch[1*], Lance G. Barrett-Lennard[2], Graeme M. Ellis[3], John K. B. Ford[3], Volker B. Deecke[4,5]

[1]*Department of Biology & W. M. Keck Center for Behavioral Biology, North Carolina State University, 127 David Clark Labs, Raleigh, NC 27695-7617, USA*

[2]*Cetacean Research Laboratory, Vancouver Aquarium, PO. Box 3232, Vancouver, BC, V6B 3X8, Canada*

[3]*Cetacean Research Program, Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia V9T 6N7, Canada*

[4]*Centre for Wildlife Conservation, University of Cumbria, Newton Rigg, Penrith, CA11 0AH, UK*

[5]*Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, St. Andrews, Fife, KY16 8LB, Scotland UK*

[*]*corresponding author's address: North Carolina State University, Department of Biology, 127 David Clark Labs, Raleigh, NC 27606-7617, USA; email: rwriesch.evolutionarybiology@gmail.com*

Human evolution has clearly been shaped by gene–culture interactions, and there is growing evidence that similar processes act on populations of non-human animals as well. Recent theoretical studies have shown that culture can be an important evolutionary mechanism due to the ability of cultural traits to spread rapidly both vertically and horizontally, resulting in decreased within-group variance and increased between-group variance. Here, we collate the extensive literature on population divergence in killer whales (*Orcinus orca*) and argue that they are undergoing ecological speciation as a result of dietary specializations. While we cannot exclude the possibility that cultural divergence predates ecological divergence, we propose that cultural differences in the form of learned behaviors between ecologically-divergent killer whale populations have resulted in varying degrees of reproductive isolation both in sympatry and allopatry and thus have the potential to lead to incipient speciation even despite ongoing low-levels of gene flow.

ADDITONAL KEYWORDS: Cetacea – culture – cultural evolution – gene-culture coevolution – vocal dialects

THE ROLE OF CULTURE IN EVOLUTION

Recent scientific advances have revolutionized our understanding of how gene-culture coevolution has shaped and influenced human evolution (e.g., Richerson & Boyd, 2005; Laland, Odling-Smee & Miles, 2010). Traditionally, it was thought that products of culture (e.g. shelter, clothing, and tools) helped humans shield themselves from other selective pressures, thus slowing down the rate of human adaptive evolution considerably. However, most scientists now agree that culture can also have the opposite effect of increasing the rate at which many human traits evolve as well as influencing the direction of selection acting on human populations (Richerson & Boyd, 2005; Hawks *et al.*, 2007; Laland *et al.*, 2010). For example, the cultural practice of cattle farming in some human cultures drove the evolution of lactose tolerance in adults (Simoons, 1978; Richerson & Boyd, 2005; Laland *et al.*, 2010) and humans from agricultural populations living on high-starch diets have a higher number of amylase gene copies (e.g. Perry *et al.*, 2007).

Consequently, there has been a recent push for interdisciplinary projects that integrate archeological and anthropological data with discoveries of human genetics and evolutionary theory to further our understanding of human evolution (Laland *et al.*, 2010). We propose that similar processes are also acting on populations of non-human animals and have far greater evolutionary consequences than previously assumed. In this review we will use the example of the killer whale (*Orcinus orca*) to illustrate how cultures and behavioral traditions can drive population divergence even in the absence of geographic isolation.

ECOLOGICAL SPECIATION AND KILLER WHALES

As an alternative to the allopatric model of speciation as a result of geographic isolation (e.g. Coyne & Orr, 2004), the idea that reproductive isolation and ultimately speciation can result from ecologically-based divergent selection has recently received considerable attention (e.g. Rundle & Nosil, 2005; Schluter, 2009). This model is referred to as ecological speciation and can apply to allopatric, parapatric, and sympatric populations, as long as divergent selection is the ultimate cause of both population differentiation and reproductive isolation (Rundle & Nosil, 2005). Strong evidence for ecological speciation has come from a variety of natural systems, laboratory experiments, comparative studies, and theoretical models (reviewed in Rundle & Nosil, 2005; Schluter, 2009).

Here, we evaluate the evidence that the largest member of the highly diverse family Delphinidae, the killer whale, is currently undergoing ecological speciation. Although generally regarded as a single species (Committee on Taxonomy, 2009; but see LeDuc, Robertson & Pitman, 2008; Morin *et al.*, 2010), numerous ecologically divergent killer whale lineages are being recognized throughout its global distribution (three in the North Pacific, four around Antarctica, and at least two in the North Atlantic; see below for more details).

Rundle and Nosil (2005) listed three components necessary for demonstrating ecological speciation: (1) an ecological source of divergent selection between populations, (2) a mechanism responsible for reproductive isolation, and (3) a genetic mechanism linking divergent selection to reproductive isolation. Here we begin by summarizing the evidence for population divergence among killer whales and outline the sources of divergent selection that appear to be responsible for population divergence. We then discuss potential causes of reproductive isolation and suggest that cultural traditions and cultural inheritance play a central role. Finally, we argue that the deterministic mechanism linking divergent selection to reproduction in killer whales may be cultural rather than genetic.

EVIDENCE FOR POPULATION DIVERGENCE AMONG KILLER WHALES

Killer whales are second only to humans as the most widely distributed mammal on earth. They inhabit all the world's oceans but greatest densities can be found in temperate and polar regions (Ford, 2009). Killer whales are the top predator in many marine ecosystems. As a species, their diet includes over 140 species of fish, squid, mammals, reptiles and birds, but different killer whale populations typically show a high degree of dietary specialisation (Ford, 2009).

In areas of high marine productivity, two or more ecologically specialized lineages, or ecotypes, of killer whales often co-occur in sympatry. Ecotypes show differences in diet,, movement patterns, pigmentation, behavior, and morphology, as well as in group size, stability and composition (Boran & Heimlich, 1999; Baird, 2000; Barrett-Lennard & Heise, 2006; Ford, 2009; Ford & Ellis, in press; see Table 1).

Sympatric ecotype assemblages are currently reported from three different geographical regions: the eastern North Pacific, the eastern North Atlantic, and Antarctica, but there is also recent evidence for sympatric ecological divergence of killer whales from around New Zealand, the Russian Far East, the western North Atlantic, and the eastern tropical Pacific (Reeves *et al.,* 2004; Fig. 1). Lack of evidence for additional killer whale ecotypes from other parts of the world's oceans is most likely an artifact of the geographically-biased research efforts.

Probably best studied are the three sympatric ecotypes inhabiting the waters of the eastern North Pacific: the so–called offshores, residents, and transients (Boran & Heimlich, 1999; Baird, 2000; Barrett-Lennard & Heise, 2006; Ford & Ellis, in press). Several geographically distinct populations exist for each ecotype. The resident ecotype, for example consists of the Southern resident population (mainly southern British Columbia and Washington State, but also Oregon and California), the Northern resident population (mainly northern British Columbia but also southeastern Alaska and Washington State; Fig. 2), and the South Alaskan resident population (Barrett-Lennard & Heise, 2006). Recent evidence suggests that there are additional resident-like populations near the Aleutian Islands (Matkin *et al.*, 2007), in the Bering Sea (Hoelzel *et al.,* 2007), and in the western North Pacific around Kamchatka (Ivkovich *et al.*, 2010). The transient ecotype is composed of the West Coast transient population (Fig. 2), the Gulf of Alaska transient population, and the 'AT1 transient' population of Prince William Sound, Alaska (Barrett-Lennard & Heise, 2006), with further putative transient populations in the Bering Sea and around the Aleutian Islands. Residents specialize on fish, in particular salmon (*Oncorhynchus* spp.), while transients prey on marine mammals and occasionally seabirds (Barrett-Lennard & Heise, 2006; Ford, 2009; Ford & Ellis, in press). Offshores probably form a single population ranging from the Aleutian Islands to California. Their full dietary spectrum and their preferred prey have yet to be fully described; however, preliminary observations suggest that they also specialize on fish, e.g. sharks and Pacific halibut (*Hippoglossus stenolepis*; Jones, 2006; Krahn *et al.*, 2007; Dahlheim *et al.*, 2008; Ford *et al.*, 2011; Ford & Ellis, in press). Besides dietary specializations, these three killer whale ecotypes also differ in a variety of other traits including group size and the degree of philopatry (Table 1).

Research suggests that up to five sympatric killer whale ecotypes are found in Antarctic waters: Type A, Type B (with a large and small form), Type C, and Type D (Fig. 3; Pitman & Ensor, 2003; Pitman, 2011; Pitman *et al.*, 2011). Again, there appears to be a general pattern of specialization on either marine mammals and birds or fish, but the dietary distinctions warrant further investigation (Pitman & Ensor, 2003; Andrews, Pitman & Balance, 2008). Type A killer whales appear to almost exclusively prey on Antarctic minke whales (*Balaenoptera bonaerensis*), while the large form of Type B (i.e., the ‘pack ice killer whale’) specialize on seals and the small form (i.e., the ‘Gerlache killer whale’) forages for penguins (Pitman, 2011; Fig. 3). Type C killer whales, on the other hand, specialize on Antarctic toothfish (*Dissostichus mawsoni*) and show what is probably the most pronounced morphological divergence within killer whales, with both sexes being considerably smaller than other killer whales (Pitman *et al.*, 2007; Pitman, 2011; Table 1; Fig. 3). Finally, a recent study by Pitman *et al*. (2011) described the sub-Antarctic killer whale, Type D killer, which clearly differs from the other Antarctic killer whales in pigmentation and morphology (Fig. 3). However, the available data are insufficient to identify whether Type D also has a specific dietary niche.

Finally, around Iceland, Shetland, and Norway, killer whales have been reported to diverge in trophic ecology as well, but again the actual dietary specializations are not yet clearly resolved (Fig. 2). While some killer whales in the North Atlantic specialize on marine mammals (Foote *et al.*, 2009; Deecke *et al.*, 2011), others specialize on fish (predominantly herring, *Clupea harengus*; Similä & Ugarte, 1993; Similä, Holst & Christensen, 1996). Stable isotope analysis of individuals with the same mitochondrial haplotype suggests that some feed at different trophic levels (Foote *et al.*, 2009), which could either point to a greater niche width for these populations or could be an indication that this dietary shift is relatively recent so that not enough time has passed for it to have resulted in a genetic signature as well. More research is warranted to resolve this important issue,

BEHAVIORAL DIVERGENCE AND KILLER WHALE CULTURES

Culture has been defined in various ways over the past decades, but the most common definitions characterize culture as population-level behavioral variation that can be transmitted vertically (from parent to offspring), oblique (from any member of an older generation to any member of a younger generation), and horizontally (within the same generation) via social learning (Laland & Janik, 2006; Danchin & Wagner, 2008; Laland & Galef, 2009). After decades of scientific debate, there is still disagreement regarding the existence of cultures in non-human animals (e.g., Laland & Galef, 2009), but some of the most famous examples proposed as animal cultures include tool-use in chimpanzees, *Pan troglodytes*, orangutans, *Pongo* spp., and bottlenose dolphins (*Tursiops* spp.), as well as songs in songbirds and humpback whales, *Megaptera novaeangliae* (Whiten *et al.*, 1999; Krützen *et al.*, 2005; Laland & Janik, 2006; Lalang & Galef, 2009; Garland *et al.*, 2011). Behavioral diversity likely to represent cultural variation has also been described in killer whales, and comprises traits such as acoustic communication, social behavior, and foraging strategies (Table 2).

The best example for such behavioral variation in killer whales comes from residents and transients off Alaska, British Columbia, and Washington State, which have been studied intensively since the 1970s (e.g. Bigg, 1982). This research has documented a complete lack of dietary overlap between the two ecotypes (based on observational studies, stomach content analysis of stranded individuals, and stable isotope analysis of blubber biopsies): in over 40 years of study, no resident has ever been found to kill and consume marine mammal prey, and no transient has been documented to take fish (e.g., Ford et al. 1998; Saulitis *et al.*, 2000; Herman *et al.*, 2005; Dahlheim & White, 2010). These dietary specializations result in differences in social structure between residents and transients with transient group sizes usually being much smaller than resident group sizes (Bigg *et al.*, 1990; Baird & Dill, 1996; Ford & Ellis, 1999; Baird, 2000).

AN EXAMPLE OF CULTURE: VOCAL BEHAVIOR IN KILLER WHALES

Killer whales produce three types of sounds: echolocation clicks are thought to function in orientation and prey detection whereas pulsed calls and whistles are communicative signals (Ford, 1989; Thomsen, Franck & Ford, 2002). While there is recent evidence for some universal acoustic signals (Rehn *et al.*, 2011), the structure and the frequency of use of most vocalizations differs strikingly between ecotypes. In the northeastern Pacific for example, mammal-hunting transient killer whales use echolocation very sparingly whereas residents, sympatric salmon specialists, echolocate frequently (Barrett-Lennard, Ford & Heise, 1996). The same applies for pulsed calls (Deecke, Ford & Slater, 2005) and whistles (Riesch & Deecke, 2011) – transients produce these almost exclusively in non-hunting contexts. Whereas salmon cannot detect killer whale sounds over significant distances, marine mammals have good underwater hearing and exhibit anti-predator behavior in response to transient calls (Deecke, Slater & Ford, 2002). Mammal-eating killer whales therefore probably reduce their vocal behavior to avoid eavesdropping by potential prey, and similar behavioral patterns have recently been revealed in mammal-hunting killer whales in the North Atlantic (Deecke *et al.,* 2011).

In addition to usage differences, the structure of killer whale vocalizations also varies among populations and social groups. Differences in the frequency content and patterning of echolocation clicks are probably related to the nature of the echolocation task and to prey hearing (Barrett-Lennard *et al.*, 1996), and thus directly related to feeding. Many pulsed calls and some whistles are highly stereotyped and can easily be assigned to call or whistle types (Ford, 1989;

Riesch, Ford & Thomsen, 2006). Variation in communicative sounds can be found on three levels. First, there is geographic variation among allopatric populations, because spatially separated populations differ in their repertoires of stereotyped pulsed calls, e.g., eastern North Pacific (Ford, 1989, 1991; Yurk *et al.*, 2002; Deecke *et al.*, 2005), western North Pacific (Filatova *et al.*, 2004), Norway (Strager, 1995), and Antarctica (Richlen & Thomas, 2008), and whistles (Riesch *et al.*, 2006; Samarra *et al.*, 2010). Second, dialect variation exists among sympatric and parapatric populations because populations of different ecotypes with overlapping home ranges also do not usually share call or whistle types. The same is true for populations of the same ecotype with adjacent or partially overlapping home ranges (Moore *et al.*, 1988; Ford, 1991; Riesch *et al.*, 2006; Riesch, Ford & Thomsen, 2008; Riesch & Deecke, 2011). Third, there is often dialect variation among social groups within a population. The Northern resident population for example contains three acoustic clans (Ford, 1991). Members belonging to different clans do not share any call types but associate frequently. They do however share stereotyped whistles (Riesch *et al.*, 2006, 2008). Call types shared within a clan typically show matriline-specific variation in call structure (Miller & Bain, 2000; Nousek *et al.,* 2006; Deecke *et al.*, 2010).

CULTURAL TRANSMISSION

The central requirement of culture is that it must be transmitted through social learning (Laland & Janik, 2006; Danchin & Wagner, 2008, 2010; Laland & Galef, 2009). In killer whales, behavioral and genetic studies have provided evidence that vocal dialects are transmitted via vocal learning rather than genetic inheritance (reviewed in Rendell & Whitehead, 2001; Janik, 2009). There is further evidence that vocal learning is not limited to vertical transmission from mother to offspring, but also takes place horizontally between matrilines with similar and different dialects (Deecke, Ford & Spong, 2000; Janik, 2009; Weiß *et al.*, 2010). Specialized hunting techniques of certain killer whale populations, such as the intentional stranding observed at Península Valdés, Argentina, and in the Crozet Islands (Table 2), have also been suggested to be transmitted via social learning from generation to generation (Hoelzel, 1991; Guinet & Bouvier, 1995), although experimental data on this are not yet available.

GENETIC DIVERGENCE, ECOTYPE FORMATION AND REPRODUCTIVE ISOLATION

Similar to various other large mammals, such as cheetahs, *Acinonyx jubatus* (O'Brien *et al.*, 1983), Antarctic fur seals, *Arctocephalus gazella* (Hoffman *et al.*, 2011), or humans (Li & Durbin, in press), killer whales are characterized by low worldwide genetic diversity both in mitochondrial and microsatellite DNA (Hoelzel *et al.*, 2002; Morin *et al.*, 2010). While such a reduction in genetic diversity is often the result of small effective population sizes and historical bottlenecks (Hoelzel *et al.*, 2002), 'cultural hitchhiking' has been proposed as an additional hypothesis to explain low mtDNA diversity in matrilineal odontocetes such as killer whales (Whitehead, 1998; but see Mesnick *et al.*, 1999).

Overall, there is no evidence for a correlation between categories of preferred dietary items and genotypes on a global scale, which suggests that local prey specializations had multiple independent origins (Hoelzel *et al.*, 2002; Morin *et al.*, 2010; Foote *et al.*, 2011b). In fact, both Morin *et al.* (2010) and Foote *et al.* (2011b) suggested that, based on mtDNA analyses, killer whales might have repeatedly migrated between the North Pacific and the North Atlantic; forming first the North Pacific transients, which are the sister group to all other killer whales.

Residents and offshores, however, originate from subsequent colonization events (Morin *et al.*, 2010; Foote *et al.*, 2011b); in other words, ecological divergence of offshores, residents, and transients could have occurred during either the allopatric or the sympatric phase, while Antarctic killer whale ecotypes are more likely to have ecologically diverged in sympatry (LeDuc *et al.*, 2008; Morin *et al.*, 2010; Foote *et al.*, 2011b).

Both mtDNA and nuclear DNA analyses confirm profound genetic differentiation of killer whale ecotypes albeit to different degrees (e.g., Hoelzel, Dahlheim & Stern, 1998; Barrett-Lennard, 2000; Hoelzel *et al.*, 2007; Morin *et al.*, 2010; Pilot, Dahlheim & Hoelzel, 2010; Foote *et al.*, 2011c). Mitochondrial DNA suggests relatively old divergence times between ecotypes with the oldest (i.e., transients) ca. 700,000 years or 40,000 generations ago (Morin *et al.*, 2010; Foote *et al.,* 2011b; Table 1). These estimates are comparable to divergence times between several evolutionarily young cetacean species (e.g., the divergence between the three right whale species (*Eubalaena* spp.) within Mysticeti, the divergence between the Ganges River and the Indus River dolphin (*Platanista* spp.) within Odontoceti, or even the divergence between the long-finned and short-finned pilot whale (*Globicephala* spp.) within Delphinidae; McGowen, Spaulding & Gatesy, 2009). On the other hand, divergence between different populations of the same ecotype appears to be more recent (e.g., Hoelzel *et al.*, 2007).

Population genetic patterns as revealed by microsatellite analyses are not as straightforward. In the eastern North Pacific, genetic distance based on nuclear DNA is greatest between resident and transient ecotypes, and F_{ST}-values clearly suggest some degree of reproductive isolation between the two (e.g., Hoelzel *et al.*, 1998, 2007; Morin *et al.,* 2010; Pilot *et al.*, 2010). A similar pattern of reproductive isolation has been described between the Antarctic Type A killer whales and both Type B and C ecotypes (LeDuc *et al.*, 2008). On the other hand, genetic distances between other ecotypes are smaller, and interbreeding appears to occur more often, for example between eastern North Pacific transients and offshores, eastern North Pacific residents and offshores, (Barrett-Lennard, 2000; Hoelzel *et al.,* 2007; Morin *et al.*, 2010; Pilot *et al.*, 2010), or Antarctic Type B and Type C killer whales (LeDuc *et al.*, 2008).

How can these slightly contradictory population genetic patterns be explained? In over 35 years of study, no case of between-culture dispersal or immigration has ever been recorded (J.K.B. Ford and G. M. Ellis, unpublished data), and even genetic analyses do not (unequivocally) suggest permanent between-ecotype dispersal (e.g., Hoelzel *et al.*, 2007; Pilot *et al.*, 2010). However, gene flow is likely to occur during rare temporary associations between individuals of different ecotypes (see discussions in Hoelzel *et al.*, 2007; Pilot *et al.*, 2010). Since offspring from such matings would then be born into and raised by their mothers' social group, we would not expect these matings to leave a mtDNA signature, but they would be detectable using nuclear markers.

As a consequence of long-term divergence and several fixed haplotype differences in mtDNA, recent studies have suggested different species or subspecies designations for certain killer whale ecotypes (LeDuc *et al.*, 2008; Morin *et al.*, 2010); however, based on the reported patterns of gene flow uncovered by nuclear markers we are not convinced that there is currently enough unambiguous evidence to warrant the designation of different killer whales species or subspecies.

CULTURAL DIVERGENCE, TYPES OF REPRODUCTIVE ISOLATION, AND SPECIATION

Recent studies have shown that pre-mating reproductive isolation can arise between different cultures even in the absence of genetic change, ultimately driving speciation (theoretical model: Gavrilets, 2004; conceptual studies: Danchin & Wagner, 2008, 2010). Some of the best empirical evidence for this comes from Darwin's finches (*Geospiza* spp.), in which song, a culturally inherited trait, is an important factor in species recognition and mate choice (e.g., Grant & Grant, 1996, 2009, 2010). Males usually learn the song from their fathers, but females prefer song types different from those of their fathers, creating an effective barrier against inbreeding (Grant & Grant, 1996). This means that a culturally inherited trait could play a crucial role in speciation by promoting genetic isolation on secondary contact (Grant & Grant 1996, 2009, 2010). We suggest that, similar to the situation in Darwin's finches, divergent cultural evolution has led to pre-zygotic and, at the very least, non-genetic post-zygotic reproductive isolation among certain killer whale populations or ecotypes, although reproductive isolation is clearly not complete (see also Boran & Heimlich, 1999; Baird, 2000).

There are at least four hypothetical mechanisms (both pre- and post-mating reproductive barriers) by which cultural divergence can lead to reproductive isolation in killer whales. First, culture could act through xenophobia if cultural imprinting is so strong that mating will not take place between individuals belonging to different cultural groupings (Danchin & Wagner, 2010). For killer whales, we propose a mechanism of positive and negative sexual/cultural imprinting acting on two levels in opposite directions that is similar to that described for humans (Rantala & Macrinkowska, 2011): On the basal level, acoustic similarity via, for example, matrilineal vocal dialects within certain populations can act as an acoustic family badge that reveals genetic relatedness (e.g., Deecke *et al.*, 2010). Negative assortative mating by dialect has been shown in some populations (Barrett-Lennard, 2000) and means that animals can reliably avoid mating with close maternal kin and thus control and reduce inbreeding processes. On the higher level, other cultural characteristics (e.g., group behavior, social structure, dietary specializations, or vocal differences between populations; reviewed in Barrett-Lennard & Heise, 2006; Ford & Ellis, in press) could act as a cultural badge that promotes endogamy within the cultural grouping by determining who an individual socializes and mates with. This process could be reinforced by differences in habitat use that limit the potential for direct interaction between different ecotypes (Guinet & Bouvier, 1995; discussion in Hoelzel *et al.*, 1998). In songbirds, local dialects are often correlated with female acoustic preferences and may lead to reproductive isolation and ultimately speciation (Price, 2008). Similar processes could be affecting killer whale mating patterns, but no direct data exist on traits influencing mate preferences or the strength of behavioral isolation in this species.

Second, cultural specializations could provide an effective barrier for between-culture dispersal by inducing temporary natural selection against immigrants (Nosil *et al*., 2005): potential dispersers would have to adjust behaviorally to the local culture and learn the local foraging behaviors (Table 2) in order to survive and reproduce with members of that culture (Danchin & Wagner, 2008, 2010). Until such cultural matching is achieved, dispersing individuals would experience drastically reduced fitness. Contrary to traditional views on ecological speciation (Rundle & Nosil, 2005) the reduction in immigrant fitness in killer whales could be based on learned behaviors rather than genetic adaptations (see also discussion in Pilot *et al.*, 2010). Whether killer whales are able to acquire non-natal cultural traits throughout their lifetime or whether there is an age-specific imprinting phase is not known. The failure to successfully reintroduce the long-term captive whale Keiko to the wild suggests that the ability to correctly assimilate cultural traditions could be age-specific (Simon *et al.*, 2009), but future studies on this are clearly warranted.

Third, cultural differences can lead to post-zygotic barriers through neutral processes such as genetic drift rather than selection (Coyne & Orr, 2004). This is particularly likely, given the small population size of most killer whale ecotypes (e.g., Hoelzel *et al.,* 2007), which increases both the potential for nonselective changes in allele frequencies as well as the speed of reproductive isolation arising through genetic drift (Coyne & Orr, 2004).

Finally, cultural differences can lead to post-zygotic barriers via gene-culture coevolution when cultural innovations change selective pressures acting on a population, eventually leading to population divergence (Danchin & Wagner, 2008; Laland *et al.*, 2010). For example, if a single individual within a population invents a new behavior that aids in exploiting a resource (e.g., intentional stranding: Lopez & Lopez, 1985; Guinet, 1991; Hoelzel, 1991; Guinet & Bouvier, 1995), this new innovation can spread rapidly within the population within a single generation as a result of vertical and horizontal transmission via social learning. Hence, cultural transmission can rapidly decrease within-group variance, while simultaneously increasing between-group variance (Lehmann & Feldman, 2008). This has the potential to effectively change the selective pressures acting on cultural groups, so that cultural change could facilitate or preempt a genetic response just like that described for human enzymes (Simoons, 1978; Whitehead, 1998; Richerson & Boyd, 2005; Hawks *et al.*, 2007; Perry *et al.*, 2007; Lehmann & Feldman, 2008; Laland *et al.,* 2010). In killer whales, differences in the dietary metabolism or respiratory and muscular systems are to be expected between different killer whale ecotypes (Foote *et al.*, 2011a). For example, a preliminary anatomical analysis suggests that resident and transient killer whales differ in skull morphology, body size, and other features, probably as a result of selection for robustness in transients to successfully hunt marine mammals (cited in Reeves *et al.*, 2004). Moreover, the physiological requirements needed to successfully perform the endurance-exhaustion technique described for killer whales foraging on tuna (Guinet *et al.*, 2007) are likely different from those needed for foraging on salmon (Ford *et al.*, 1998) or marine mammals (Miller, Shapiro & Deecke, 2010). Other genetic changes similar to those found in humans are likely, but they will have to be the focus of future functional genomic research. In particular, we propose that next generation sequencing approaches could help uncover genes that are the target of selection in different killer whale ecotypes (see also Foote *et al.*, 2011a). Candidate genes for this could be identified in model organisms for which the entire genome has been sequenced (e.g. humans, or mice).

Killer whales of different ecotypes and from different geographic regions successfully interbreed in captivity (Bowles, Young & Asper, 1988; Duffield *et al.*, 1995), ruling out genetic incompatibility (i.e., hybrid inviability), at least on the grossest level. However, with the scientific data available to us, we were unable to discern if other genetic incompatibilities (e.g., hybrid sterility) applied to offspring sired by parents of different ecotypes (but see for example URL 1 for an account of offspring sired by hybrid parents). If killer whale ecotypes have already evolved certain co-adapted genes, reduced hybrid fitness, for example in the form of lower growth rates or the inability to process certain food items, could already be possible but would only become obvious under natural conditions.

Killer whales appear to be a good example of behavioral isolation evolving far ahead of hybrid inviability or sterility (Coyne & Orr, 2004; see Price, 2008 for a discussion of this phenomenon in birds). However, in theory matrilineal behavioral preferences may be ephemeral and reversible (see discussion in LeDuc *et al.*, 2008). In fact, reversal of the observed processes of differentiation due to hybridization or homogenization have been observed between different ecotypes in other well-established model systems such as sticklebacks and cichlids (Taylor *et al.*, 2006; Seehausen *et al.*, 2008; Nosil, Harmon & Seehausen*,* 2009; Behm, Ives & Boughman, 2010), and there is good evidence for gene flow between ecotypes/populations in killer whales as well (e.g., Hoelzel *et al.,* 2007; Pilot *et al.*, 2010). Nonetheless, recent studies have demonstrated that speciation is possible despite the presence of gene flow (e.g., Dieckmann & Doebeli, 1999; Via, 2009; de León *et al.*, 2010). Clearly, different killer whale ecotypes fall into different positions along the continuum between panmixia and complete reproductive isolation, and none seem to have yet achieved full reproductive isolation. Because of this, killer whales provide an interesting case study into the factors that promote or constrain ecotype movement along the speciation continuum towards ecological speciation (e.g., Hendry, 2009; Nosil *et al.*, 2009). For example, what will happen if certain populations fall below a critical population size, or if no individual of breeding age for one sex were available? In other word, whether speciation will in fact occur depends on whether divergence exceeds the ecotype/population extinction rate. We could be witnessing the early stages of an adaptive radiation of killer whales whereby a variety of incipient species are beginning to exploit diverse ecological niches, or conversely, we could be looking at an old and ongoing process by which periodically new ecotypes form and wink out (Barrett-Lennard, 2011).

CAN CULTURAL TRADITIONS LEAD TO STABLE REPRODUCTIVE ISOLATION?

Three incidents may help shed some light on this question. The first one is the report of three transient killer whales captured off British Columbia in 1970. For the first 75 days of captivity, all three individuals refused to eat the fish provided by their captors, which eventually resulted in death by starvation of one killer whale. Only after that event did the other two transients begin eating fish, but they immediately reverted back to foraging on marine mammals after their release back to the wild (Ford & Ellis, 1999). For two other transients from the same capture an interesting case of intercultural transmission occurred when they, after 24 days of self-induced starvation, were put in a pool with a Southern resident and were both feeding on herring within hours after being passed fish by the resident (G. M. Ellis, unpublished data). The third example stems from observations made following the 'Exxon Valdez' oil spill in 1989. AT1 pod (a small, genetically distinct population of transients from Prince William Sound, Alaska) lost 9 members (41%) of their social group including several reproductive females after the spill, and an additional 4 males after 2000 (Matkin *et al.*, 2008). Since no successful recruitment has taken place in this social group since 1984, group size is now reduced to 7 individuals with only two reproductive females and one adult male (Matkin *et al.*, 2008). One possibility enabling group survival would be for AT1 to join another transient population, for example the Gulf of Alaska transients; however, there is so far no indication of this happening (Matkin *et al.*, 2008). Thus, it appears that cultural traditions in killer whales can be a strong reproductive isolation mechanism that is stable even in the face of individual death or potential population extinction.

CONCLUSIONS

Our review reveals multiple trait divergence among killer whales, including population divergence in behavior, pigmentation patterns, morphology, dietary specializations, and genetics. While there are still many open questions concerning the degree of this divergence and the strength of reproductive isolation, the overall pattern that emerges strongly suggests that ecological speciation could be the driving force behind global killer whale diversity. Dietary specialization is likely to have resulted in divergent selection between populations thus fulfilling the first requirement for ecological speciation. Behavioral isolation due to sexual imprinting is the most likely candidate for a current mechanism for reproductive isolation (the second requirement; Rundle & Nosil, 2005). Although the currently available data did not allow us to identify a genetic mechanism linking divergent selection to reproductive isolation, we argue that this is not strictly necessary. What is needed is a deterministic mechanism that links divergent selection to reproductive isolation. As an alternative to strict genetic inheritance, another heritable unit —culture— clearly provides this deterministic mechanism in killer whales.

An interesting alternative, however, could be that cultural divergence may predate ecological divergence in killer whales, meaning that they may not be undergoing ecological speciation *per se*, but rather “cultural speciation” as outlined by Gavrilets (2004); a combination of cultural and ecological mechanisms is also possible.. Future studies are needed to shed more light on which came first, cultural or ecological divergence.

While killer whales are probably unusual in the extent to which culturally-driven selection has driven diversification and ultimately speciation (e.g., there is so far no evidence that culture has led to evolutionary significant levels of reproductive isolation in humans), culture and behavioral traditions also appear to be important features in the biology of various other cetacean species, such as humpback whales, sperm whales (*Physeter macrocephalus*), and bottlenose dolphins (reviewed in Rendell & Whitehead, 2001; Laland & Galef, 2009). Hence, the combination of cultural and ecological divergence may have been the main driving force behind some of the observed species diversity in the order Cetacea (Berta, Sumich & Kovacs, 2006). Most importantly, however, such divergence may not be restricted to cetaceans and to a greater or lesser degree may be affecting any species (e.g., birds), in which socially transmitted behaviors have fitness consequences. While most of that divergence took place in the past, killer whales provide an excellent opportunity to study patterns of divergence and diversification in action. However, these patterns of current ecotype diversity in killer whales also have important implications for conservation, because they raise questions about the evolutionary significant units that warrant protection (e.g., Moritz, 1994; Hoelzel, 1998; Ryan, 2006; Whitehead, 2010).

Because many of their behavioral traits, such as vocal dialects, can be easily quantified, killer whales provide an exceptional opportunity to investigate how cultures can affect the evolutionary trajectories of populations, an aspect often ignored in the conceptual literature on speciation processes (but see Coyne & Orr, 2004; Price, 2008). Recent studies have demonstrated that culture plays an important role in shaping human evolution via culture-gene coevolution (Simoons, 1978; Richerson & Boyd, 2005; Hawks *et al.*, 2007; Perry *et al.*, 2007; Laland *et al.*, 2010). However, the evidence we provide for killer whales suggests that culture and behavioral traditions could have far greater evolutionary consequences than previously assumed (see also Boran & Heimlich, 1999; Baird, 2000). Following the example of Danchin & Wagner (2010), we therefore propose that the cultural component of behavior should be included along with phenotypic plasticity and epigenetics in a revised form of the modern synthesis of the study of evolution (see also Pigliucci, 2007; Pennisi, 2008). Furthermore, we propose that the third component of ecological speciation be extended to include both genes and culture as mechanisms linking divergent selection and reproductive isolation.

Finally, recent years have seen the emergence of more specific theoretical models on how ecologically-based divergent natural selection can result in population divergence and ultimately speciation (e.g., Gavrilets *et al.*, 2007; Sadedin *et al.*, 2009). Future research on killer whales could—to the extent that this is possible with field studies on such a large marine organism—try to specifically test some of these models and their predictions.

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Table 1. Divergent traits between identified killer whale ecotypes.

Region	Ecotype comparison	Divergent traits								Estimated time since divergence (mtDNA)	References
		AB	**AS**	**D/F**	**G**	**M**	**MP**	**P**	**SS**		
NE Pacific	residents vs. transients	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	~700.000 yrs	Baird & Whitehead, 2000; Deecke *et al.*, 2005; Barrett-Lennard, 2006; Morin *et al.*, 2010; Pilot *et al.*, 2010; Riesch & Deecke, 2011; Ford & Ellis, in press
	residents vs. offshores	n/a	Yes	Yes	Yes	Yes	Yes	Yes	Yes	>150.000 yrs	Barrett-Lennard & Heise, 2006; Dahlheim *et al.*, 2008; Morin *et al.*, 2010; Pilot *et al.*, 2010; Ford *et al.*, 2011; Ford & Ellis, in press
	transients vs. offshores	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	~700.000 yrs	Barrett-Lennard & Heise, 2006; Dahlheim *et al.*, 2008; Morin *et al.*, 2010; Pilot *et al.*, 2010; Ford *et al.*, 2011; Ford & Ellis, in press
Antarctica	Type A vs. Type B (Pack Ice)	n/a	n/a	?	Yes	n/a	n/a	Yes	?	>150.000 yrs	Pitman & Ensor, 2003; Morin *et al.*, 2010; Pitman, 2011

Type A vs. Type B (Gerlache)	n/a	n/a	?	Yes	n/a	n/a	Yes	?	>150.000 yrs.	Pitman & Ensor, 2003; Morin *et al.*, 2010; Pitman, 2011
Type A vs. Type C	n/a	n/a	Yes	Yes	Yes	?	Yes	Yes	>150.000 yrs	Pitman & Ensor, 2003; Pitman *et al.*, 2007; Morin *et al.*, 2010
Type A vs. Type D	n/a	n/a	?	n/a	Yes	?	Yes	n/a	n/a	Pitman *et al.*, 2011
Type B (Pack Ice) vs. Type B (Gerlache)	n/a	n/a	Yes	n/a	n/a	n/a	n/a	Yes	n/a	Pitman, 2011
Type B (Pack Ice) vs. Type C	n/a	n/a	Yes	Yes	Yes	?	Yes	Yes	~150.000 yrs	Pitman & Ensor, 2003; Pitman *et al.*, 2007; Andrews *et al.*, 2008; Morin *et al.*, 2010; Pitman, 2011
Type B (Pack Ice) vs. Type D	n/a	n/a	?	n/a	Yes	?	Yes	n/a	n/a	Pitman *et al.*, 2011; Pitman, 2011
Type B (Gerlache) vs. Type C	n/a	n/a	Yes	Yes	Yes	?	Yes	Yes	~150.000 yrs	Pitman & Ensor, 2003; Pitman *et al.*, 2007; Andrews *et al.*, 2008; Morin *et al.*, 2010; Pitman, 2011

	Type B (Gerlache) vs. Type D	n/a	n/a	?	n/a	Yes	?	Yes	n/a	n/a	Pitman *et al.*, 2011; Pitman, 2011
	Type C vs. Type D	n/a	n/a	n/a	n/a	Yes	?	Yes	n/a	n/a	Pitman *et al.*, 2011; Pitman, 2011
NE Atlantic	generalists vs. mammal-eaters	n/a	n/a	Yes	n/a	Yes	Yes	Yes	n/a	n/a	Similä *et al.*, 1996; Wolkers *et al.*, 2007; Foote *et al.*, 2009, 2011c; Morin *et al.*, 2010

AB: acoustic behavior; AS: acoustic signals; D/F: diet and foraging behavior; G: genetics, M: morphology; MP: movement/diving patterns; P: pigmentation; SS: social structure; RI: reproductive isolation; ?: inconclusive, but preliminary studies suggest divergence; n/a: data not available

Table 2. Cultural traditions of killer whale populations from around the globe.

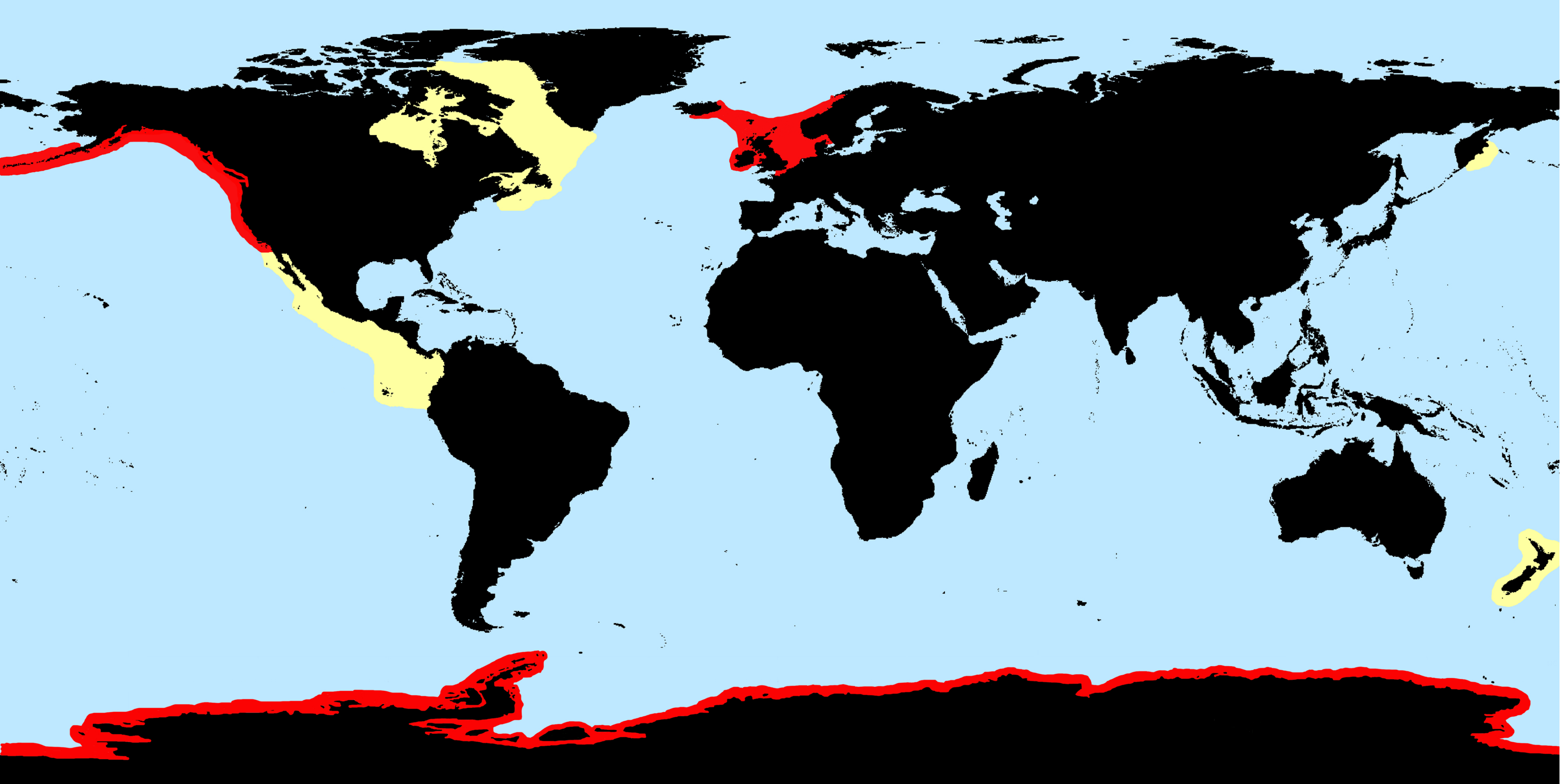
Phenomenon	Behavioral context	Geographic Region	References
Call dialects	all behaviors	NE Pacific	Ford, 1989, 1991; Yurk *et al.*, 2002; Deecke *et al.*, 2005; Ford & Ellis, in press
Greeting ceremonies	social behavior	NE Pacific	Osborne, 1986
Whistle dialects	social behavior	NE Pacific	Riesch *et al.*, 2006; Riesch & Deecke, 2011
Beach rubbing	social behavior	NE Pacific	Ford, 1989; Ford, Ellis & Balcomb, 2000
Benthic foraging	foraging behavior	SW Pacific	Visser, 1999
Carousel feeding	foraging behavior	NE Atlantic	Similä & Ugarte, 1993; Domenica *et al.*, 2000; Nottestad & Similä, 2001; Simon *et al.*, 2005
		NW Pacific	Tarasyan *et al.*, 2005
Endurance-exhaustion hunting	foraging behavior	Atlantic	Guinet *et al.*, 2007
Exploitation of longline fishing	foraging behavior	widespread	Secchi & Vaske, 1998; Nolan & Liddle, 2000; Visser, 2000
Intentional stranding	foraging behavior	SW Atlantic	Lopez & Lopez, 1985; Hoelzel, 1991
		S Indian Ocean	Guinet, 1991; Guinet & Bouvier, 1995
Wave-washing	foraging behavior	Southern Ocean	Smith *et al.*, 1981; Visser *et al.*, 2008; Pitman, 2011 ; Pitman & Durban, in press

FIGURE LEGENDS

Figure 1. World map with approximate distributions of known sympatric killer whale ecotypes in red and potential sympatric ecotypes in eggshell.

Figure 2. Known killer whales ecotypes of the northern hemisphere. Note the size, pigmentation, and dorsal fin shape differences between the sexes (males left, females right), but also between ecotypes. Artwork by Uko Gorter.

Figure 3. Known killer whales ecotypes of the southern hemisphere. Note the size, pigmentation, and dorsal fin shape differences between the sexes (males left, females right), but also between ecotypes. Artwork by Uko Gorter.



KILLER WHALES

Northern Hemisphere ecotypes & forms