

REVIEW ARTICLE

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

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Human evolution has clearly been shaped by gene–culture interactions, and there is growing evidence that similar processes also act on populations of non-human animals. Recent theoretical studies have shown that culture can be an important evolutionary mechanism because of the ability of cultural traits to spread rapidly both vertically, obliquely, 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. Although we cannot exclude the possibility that cultural divergence pre-dates ecological divergence, we propose that cultural differences in the form of learned behaviours between ecologically divergent killer whale populations have resulted in sufficient reproductive isolation even in sympatry to lead to incipient speciation. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **106**, 1–17.

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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 & Myles, 2010). Traditionally, it was thought that products of culture (e.g. shelter, clothing, and tools) helped humans shield themselves from other selective pres-

ures, 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 populations 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

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have more copies of the amylase gene (e.g. Perry *et al.*, 2007).

Consequently, there has been a recent push for interdisciplinary projects that integrate archaeological 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 can have far greater evolutionary consequences than has previously been assumed. In this review we will use the example of the killer whale (*Orcinus orca*) to illustrate how cultures and behavioural traditions can drive population divergence even in the absence of geographic isolation.

ECOLOGICAL SPECIATION AND *ORCINUS ORCA*

As an alternative to the allopatric model that explains speciation as the 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 by Rundle & Nosil, 2005; Schluter, 2009).

Here, we evaluate 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 *O. orca* lineages are recognized throughout its global distribution (three in the North Pacific, five around Antarctica, and at least two in the North Atlantic; see below for more details).

Rundle & Nosil (2005) list three components necessary for demonstrating ecological speciation: (1) an ecological source of divergent selection between populations; (2) a form of reproductive isolation; and (3) a genetic mechanism linking divergent selection to reproductive isolation. Here, we begin by summarizing the evidence for population divergence among *O. orca* and outline the sources of divergent selection that appear to be responsible for population diver-

gence. 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 *O. orca* may be cultural rather than genetic.

EVIDENCE FOR POPULATION DIVERGENCE AMONG KILLER WHALES

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

In areas of high marine productivity, two or more ecologically specialized lineages, or ecotypes, of *O. orca* often co-occur in sympatry. Ecotypes show differences in diet, movement patterns, pigmentation, behaviour, and morphology (Figs 1, 2), as well as in the size, stability, and composition of social groups (Heimlich & Boran, 1999; Baird, 2000; Barrett-Lennard & Heise, 2006; Ford, 2009; Ford & Ellis, 2012; 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 *O. orca* from around New Zealand, the Russian Far East, the western North Atlantic, and the eastern tropical Pacific (Reeves *et al.*, 2004; ranges shown in Fig. 3). The lack of evidence for additional killer whale ecotypes from other parts of the world's oceans is most likely a consequence of the limited research effort in these regions.

Best studied are the three sympatric ecotypes inhabiting the waters of the eastern North Pacific, called offshores, residents, and transients (Heimlich & Boran, 1999; Baird, 2000; Barrett-Lennard & Heise, 2006; Ford & Ellis, 2012). Several geographically distinct populations exist for each ecotype (Barrett-Lennard & Heise, 2006). The resident ecotype, for example, consists of the southern resident population (~88 individuals, URL 1, 2011; mainly in southern British Columbia and Washington State, but also in Oregon and California), the northern resident population (~260 individuals, Ellis, Towers & Ford, 2011; mainly in northern British Columbia, but also in south-eastern Alaska and Washington State; Fig. 1), and the South Alaskan resident population (> 700 individuals, Matkin & Durban, 2011; from

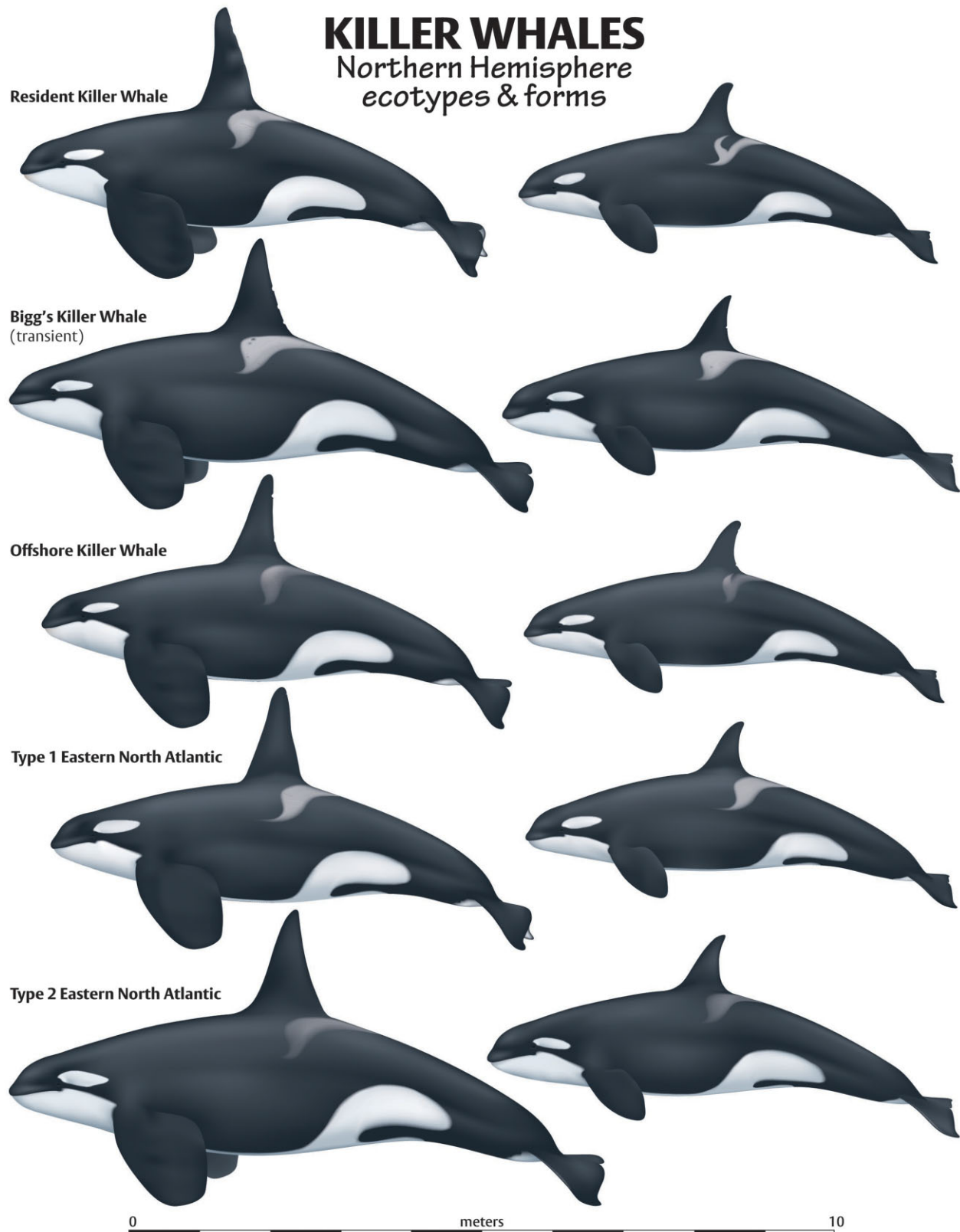


Figure 1. Known killer whale (*Orcinus orca*) ecotypes of the Northern Hemisphere. Note the size, pigmentation, and dorsal fin shape differences between the sexes (males left; females right), but also between ecotypes. Artwork by Uko Gorter.

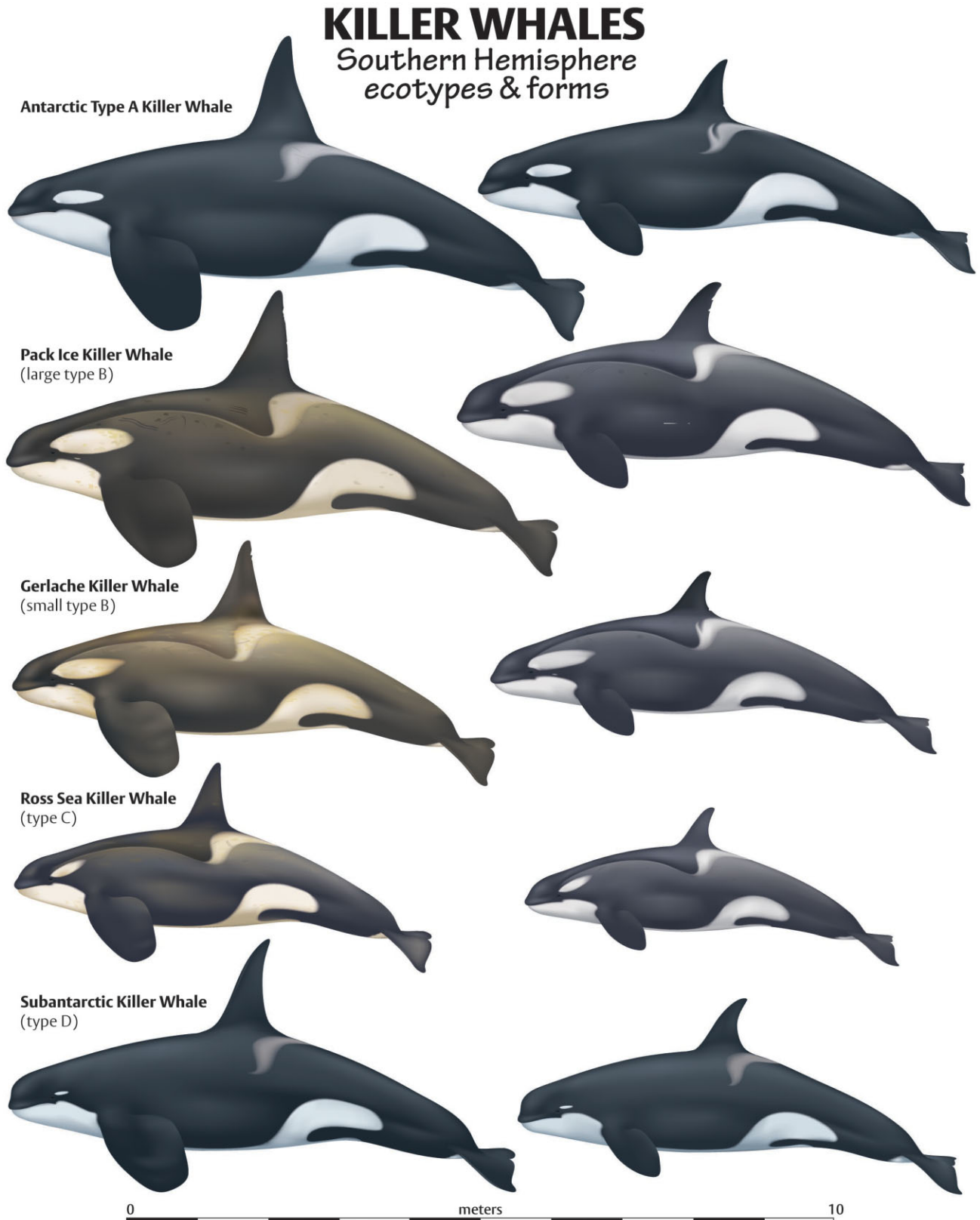


Figure 2. Known killer whale (*Orcinus orca*) ecotypes of the Southern Hemisphere. Note the size, pigmentation, and dorsal fin shape differences between the sexes (males left; females right), but also between ecotypes. Artwork by Uko Gorter.

Table 1. Divergent traits between identified killer whale (*Orcinus orca*) 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	Baird & Whitehead (2000); Deecke <i>et al.</i> (2005); Barrett-Lennard & Heise (2006); Morin <i>et al.</i> (2010); Pilot <i>et al.</i> (2010); Ford & Ellis (2012); Riesch & Deecke (2011)
	Residents vs offshores	?	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Barrett-Lennard & Heise (2006); Dahlheim <i>et al.</i> (2008); Morin <i>et al.</i> (2010); Pilot <i>et al.</i> (2010); Ford & Ellis (2012); Ford <i>et al.</i> (2011)
	Transients vs offshores	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Barrett-Lennard & Heise (2006); Dahlheim <i>et al.</i> (2008); Morin <i>et al.</i> (2010); Pilot <i>et al.</i> (2010); Ford & Ellis (2012); Ford <i>et al.</i> (2011)
Antarctica	Type A vs type B (pack ice)	?	?	P	Yes	?	?	Yes	P	Pitman & Ensor (2003); Morin <i>et al.</i> (2010); Pitman (2011)
	Type A vs type B (Gerlache)	?	?	P	Yes	?	?	Yes	P	Pitman & Ensor (2003); Morin <i>et al.</i> (2010); Pitman (2011)
	Type A vs type C	?	?	Yes	Yes	Yes	P	Yes	Yes	Pitman & Ensor (2003); Pitman <i>et al.</i> (2007); Morin <i>et al.</i> (2010)
	Type A vs type D	?	?	P	?	Yes	P	Yes	?	Pitman <i>et al.</i> (2011)
	Type B (pack ice) vs type B (Gerlache)	?	?	Yes	?	?	?	?	?	Pitman (2011)
	Type B (pack ice) vs type C	?	?	Yes	Yes	Yes	P	Yes	Yes	Pitman & Ensor (2003); Pitman <i>et al.</i> (2007); Andrews <i>et al.</i> (2008); Morin <i>et al.</i> (2010); Pitman (2011)
NE Atlantic	Type B (pack ice) vs type D	?	?	P	?	Yes	P	Yes	?	Pitman <i>et al.</i> (2011); Pitman (2011)
	Type B (Gerlache) vs type C	?	?	Yes	Yes	Yes	P	Yes	Yes	Pitman & Ensor (2003); Pitman <i>et al.</i> (2007); Andrews <i>et al.</i> (2008); Morin <i>et al.</i> (2010); Pitman (2011)
	Type B (Gerlache) vs type D	?	?	P	?	Yes	P	Yes	?	Pitman <i>et al.</i> (2011); Pitman (2011)
	Type C vs type D	?	?	?	?	Yes	P	Yes	?	Pitman <i>et al.</i> (2011); Pitman (2011)
	Generalists vs mammal-eaters	?	?	Yes	?	Yes	Yes	Yes	?	Similä <i>et al.</i> (1996); Volkens <i>et al.</i> (2007); Foote <i>et al.</i> (2009, 2011c); Morin <i>et al.</i> (2010)

AB, acoustic behaviour; AS, acoustic signals; D/F, diet and foraging behaviour; G, genetics; M, morphology; MP, movement/diving patterns; P, pigmentation; SS, social structure; P, inconclusive, but preliminary studies suggest divergence; ?, data not available.

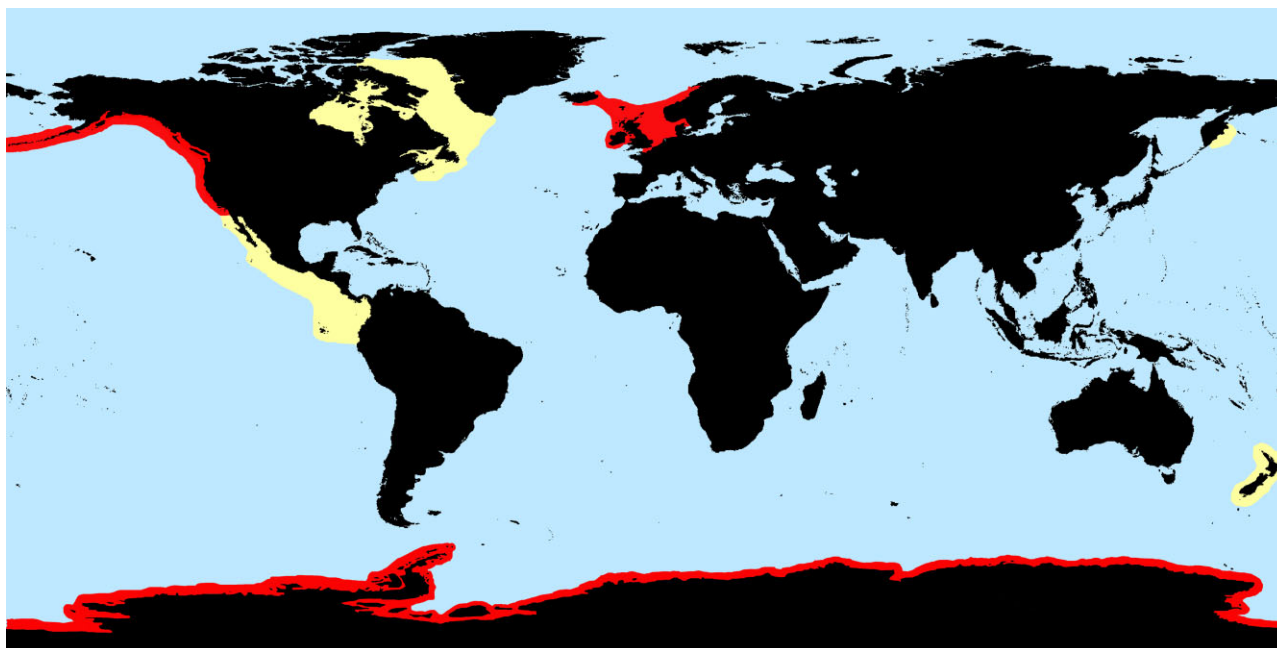


Figure 3. World map with approximate distributions of known sympatric killer whale (*Orcinus orca*) ecotypes in red (dark grey in print) and potential sympatric ecotypes in yellow (white in print).

eastern South Alaska west to the Alaska Peninsula). Recent evidence suggests that there are additional resident-like populations near the Aleutian Islands (Matkin *et al.*, 2007; > 1500 individuals, Matkin & Durban, 2011), 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 (~250 individuals, URL 2, 2011; Fig. 1), the Gulf of Alaska transient population (< 100 individuals, Matkin & Durban, 2011), and the AT1 transient population of Prince William Sound, Alaska (around seven individuals, Barrett-Lennard & Heise, 2006; Matkin *et al.*, 2008), with further putative transient populations in the Bering Sea and around the Aleutian Islands. Residents specialize on fish, in particular on salmon (*Oncorhynchus* spp.), whereas transients prey on marine mammals and occasionally seabirds (Barrett-Lennard & Heise, 2006; Ford, 2009; Ford & Ellis, 2012). Offshores probably form a single population ranging from the Aleutian Islands to California. Their dietary spectrum and their preferred prey have yet to be fully described, but preliminary observations suggest that they also specialize on fish such as Pacific sleeper shark (*Somniosus pacificus*) and Pacific halibut (*Hippoglossus stenolepis*); (Jones, 2006; Krahn *et al.*, 2007; Dahlheim *et al.*, 2008; Ford & Ellis, 2012; Ford *et al.*, 2011). In addition to dietary specialization, 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 *O. orca* ecotypes are found in Antarctic waters (25 000–27 000 individuals; Branch & Butterworth, 2001): type A, type B (with a large and small form), type C, and type D (Fig. 2; 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 & Ballance, 2008). Type-A killer whales appear to prey almost exclusively on Antarctic minke whales (*Balaenoptera bonaerensis*), whereas the large form of type B (the ‘pack-ice killer whale’) specializes on seals, and the small form (the ‘Gerlache killer whale’) hunts penguins (Pitman, 2011; Fig. 2). 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 *O. orca*, with both sexes being considerably smaller than other ecotypes (Pitman *et al.*, 2007; Pitman, 2011; Fig. 2; Table 1). Finally, a recent study by Pitman *et al.* (2011) described the sub-Antarctic type D, which clearly differs from all other Antarctic ecotypes in pigmentation and morphology (Fig. 2). However, the available data are insufficient to identify whether type D also has a specific dietary niche.

Around Iceland, Shetland, and Norway, *O. orca* have also been reported to diverge in trophic ecology, but again the actual dietary specializations are not yet clearly resolved (Fig. 2). Whereas some killer

Table 2. Cultural traditions of killer whale (*Orcinus orca*) populations from around the globe

Phenomenon	Behavioural context	Geographic region	References
Call dialects	All behaviours	NE Pacific	Ford (1989, 1991); Yurk <i>et al.</i> (2002); Deecke <i>et al.</i> (2005); Ford & Ellis (2012)
Greeting ceremonies	Social behaviour	NE Pacific	Osborne (1986)
Whistle dialects	Social behaviour	NE Pacific	Riesch <i>et al.</i> (2006); Riesch & Deecke (2011)
Beach rubbing	Social behaviour	NE Pacific	Ford (1989); Ford, Ellis & Balcomb (2000)
Benthic foraging	Foraging behaviour	SW Pacific	Visser (1999)
Carousel feeding	Foraging behaviour	NE Atlantic	Similä & Ugarte (1993); Domenici <i>et al.</i> (2000); Nottestad & Similä (2001); Simon <i>et al.</i> (2005)
		NW Pacific	Tarasyan <i>et al.</i> (2005)
Endurance–exhaustion hunting	Foraging behaviour	Atlantic	Guinet <i>et al.</i> (2007)
Exploitation of longline fishing	Foraging behaviour	widespread	Secchi & Vaske (1998); Nolan & Liddle (2000); Visser (2000)
Intentional stranding	Foraging behaviour	SW Atlantic	Lopez & Lopez (1985); Hoelzel (1991)
		S Indian Ocean	Guinet (1991); Guinet & Bouvier (1995)
Wave-washing	Foraging behaviour	Southern Ocean	Smith <i>et al.</i> (1981); Visser <i>et al.</i> (2008); Pitman (2011); Pitman & Durban (2012)

whales in the North Atlantic appear to 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, 2011c; but see Morin *et al.*, 2010), which could either point to a greater niche width for these populations or could be an indication that this dietary shift is relatively recent, and has not yet resulted in genetic differentiation. More research is warranted to resolve this important issue.

BEHAVIOURAL DIVERGENCE AND KILLER WHALE CULTURES

Culture has been defined in various ways over the past decades, but the most common definitions characterize it as population-level behavioural variation that can be transmitted vertically (from parent to offspring), obliquely (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 little disagreement regarding the existence of cultures in non-human animals (but see Laland & Galef, 2009). Some of the most famous examples of animal cultures are tool-use in chimpanzees, *Pan troglodytes*, orangutans, *Pongo* spp., and bottlenose dolphins (*Tursiops* spp.), and

songs in songbirds and humpback whales (*Megaptera novaeangliae*; Whiten *et al.*, 1999; Krützen *et al.*, 2005; Laland & Janik, 2006; Laland & Galef, 2009; Garland *et al.*, 2011). Culturally transmitted behavioural diversity has also been described in *O. orca*, and comprises traits such as acoustic communication, social behaviour, and foraging strategies (Table 2).

The best example for such behavioural variation in *O. orca* comes from residents and transients off Alaska, British Columbia, and Washington State. These ecotypes have been studied intensively since the 1970s (e.g. Bigg, 1982), and 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 BEHAVIOUR IN *ORCINUS ORCA*

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). Although there is recent evidence for some universal acoustic signals (Rehn *et al.*, 2011), the structure and frequency of use of most vocalizations differs strikingly between ecotypes. In the north-eastern Pacific, for example, transient mammal-hunting *O. orca* use echolocation very sparingly, whereas resident, 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 *O. orca* sounds over significant distances, marine mammals have good underwater hearing, and exhibit anti-predator behaviour in response to transient calls (Deecke, Slater & Ford, 2002). Mammal-eating killer whales therefore probably reduce their vocal behaviour to avoid eavesdropping by potential prey, and similar behavioural patterns have recently been revealed in mammal-hunting *O. orca* in the North Atlantic (Deecke *et al.*, 2011).

In addition to differences in usage, the structure of *O. orca* 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 are 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). Allopatric populations also differ in their whistle repertoires (Riesch *et al.*, 2006; Samarra *et al.*, 2010). Second, sympatric and parapatric populations exhibit dialect variation because populations of different ecotypes with overlapping home ranges also do not share call or whistle types. The same is usually 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 *O. orca*, behavioural 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 matriline with similar and different dialects (Deecke, Ford & Spong, 2000; Janik, 2009; Weiß *et al.*, 2010). The 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, 2011), killer whales are characterized by low worldwide genetic diversity, both in mitochondrial and microsatellite DNA (Hoelzel *et al.*, 2002; Morin *et al.*, 2010). Whereas 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 mitochondrial DNA (mtDNA) diversity in matrilineal odontocetes such as *O. orca* (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) suggest that, based on mtDNA analyses, killer whales might have repeatedly migrated

between the North Pacific and the North Atlantic. According to this scenario, transients, who are the sister group to all other killer whales, became isolated following an early colonization event, and residents and offshores originate from more recent colonization events (Morin *et al.*, 2010; Foote *et al.*, 2011b). Ecological divergence of offshores, residents, and transients could therefore have occurred in either allopatry or sympatry. In contrast, the divergence of multiple Antarctic ecotypes is more likely to have occurred in sympatry than allopatry (LeDuc *et al.*, 2008; Morin *et al.*, 2010; Foote *et al.*, 2011b).

Both mtDNA and nuclear DNA analyses confirm profound genetic differentiation of *O. orca* 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) having diverged ~ 700 000 years or 40 000 generations ago (Morin *et al.*, 2010; Foote *et al.*, 2011b; Table 1). These estimates are comparable with divergence times between several evolutionarily young cetacean species [e.g. the divergence between the three right whale species (*Eubalaena* spp.), the divergence between the Ganges River and the Indus River dolphin species (*Platanista* spp.), or 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, the genetic distance based on nuclear DNA is greatest between resident and transient ecotypes, and F_{ST} values (fixation index; Weir & Cockerham, 1984) 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 -C ecotypes (LeDuc *et al.*, 2008).

How can these contradictory population genetic patterns be explained? In over 35 years of study, no case of between-culture dispersal or immigration has been recorded (J.K.B. Ford and G. M. Ellis, unpubl.

data), and genetic analyses do not provide unequivocal evidence for 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). As offspring from such mating would then be born into and raised by their mother's social group, we would not expect these matings to leave an mtDNA signature, whereas they will 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 revealed by the analysis of nuclear markers, we are not convinced that there is currently enough unambiguous evidence to warrant the designation of different 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, Gavrillets, 2004; conceptual studies, Danchin & Wagner, 2008, 2010). Some of the best empirical evidence for this comes from Darwin's finches (*Geospiza* spp.), for 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 that differ 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 not complete (see also Heimlich & Boran, 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 *O. orca*. 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 *O. orca*, we propose that a mechanism of positive and negative sexual/cultural imprinting acts on two levels but in opposite directions, similar to that described for humans (Rantala & Marcinkowska, 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. On the higher level, other cultural characteristics (e.g. group behaviour, social structure, dietary specializations, or vocal differences between populations; reviewed in Barrett-Lennard & Heise, 2006; Ford & Ellis, 2012) 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 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 *O. orca* mating patterns, but no direct data exist on traits influencing mate preferences or the strength of behavioural isolation in this species.

Second, cultural specializations could provide an effective barrier for between-culture dispersal by inducing temporary natural selection against immigrants (Nosil, Vines & Funk, 2005): potential dispersers would have to adjust behaviourally to the local culture, and learn the local foraging behaviours (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 behaviours rather than genetic adaptations (see also discussion in Pilot *et al.*, 2010). Whether *O. orca* 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 further research into this is 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 non-selective 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 behaviour that aids in exploiting a resource (e.g. intentional stranding, Lopez & Lopez, 1985; Guinet, 1991; Hoelzel, 1991; Guinet & Bouvier, 1995), this 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 pre-empt a genetic response, just as 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 *O. orca*, differences in metabolism or respiratory and muscular systems are to be expected between different ecotypes (Foote *et al.*, 2011a). For example, a preliminary anatomical analysis suggests that residents and transients 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 *O. orca* foraging on tuna (Guinet *et al.*, 2007) are likely to differ 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 (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).

Orcinus orca 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 most coarse 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 for an account of offspring sired by hybrid parents in captivity, see URL 3 2011). If killer whale ecotypes have already evolved certain co-adapted genes, reduced hybrid fitness, for example in the form of lower growth rates or a reduced ability to process certain food items, is possible, but would only manifest itself under natural conditions.

Orcinus orca appears to be a good example of behavioural isolation evolving far ahead of hybrid inviability or sterility (Coyne & Orr, 2004; for a discussion of this phenomenon in birds, see Price, 2008). However, in theory, matrilineal behavioural preferences may be ephemeral and reversible (see discussion in LeDuc *et al.*, 2008). In fact, reversal of the observed processes of differentiation as a result of 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 also good evidence for gene flow between ecotypes/populations in *O. orca* (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, *O. orca* provides 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 would happen if certain populations fall below a critical population size, or if no individual of breeding age for one sex is available? Whether speciation will 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 continuing process by which new ecotypes periodically form and become extinct again (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 animal. 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, unpubl. data). The third example stems from observations made following the 'Exxon Valdez' oil spill in 1989. After the spill, pod AT1 (a small, genetically distinct population of transients from Prince William Sound, Alaska) lost nine members (41%) of their social group, including several reproductive females, and an additional four males died after 2000 (Matkin *et al.*, 2008). As no successful recruitment has taken place into this social group since 1984, the group size is now reduced to seven 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 *O. orca* can be a strong reproductive isolation mechanism that is stable even in the face of potential population extinction.

CONCLUSION

Our review highlights multiple trait divergences among *O. orca*, including population divergence in behaviour, pigmentation patterns, morphology, dietary specializations, and genetics. Although 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 is 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. Behavioural isolation resulting from sexual imprinting is the most likely candidate for a mechanism for reproductive isolation (the second requirement of 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 pre-date ecological divergence in *O. orca*, meaning that they may not be undergoing ecological speciation per se, but rather ‘cultural speciation’, as outlined by Gavrillets (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.

Whereas *O. orca* are probably unusual in the extent to which culturally-driven selection has driven diversification, and ultimately speciation (e.g. there is no evidence so far that culture has led to evolutionary significant levels of reproductive isolation in humans), culture and behavioural 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, but may be affecting any species in which socially transmitted behaviours have fitness consequences. Although most of the divergence took place in the past, killer whales provide an excellent opportunity to study patterns of divergence and diversification in action. In addition, these patterns of current ecotype diversity in *O. orca* 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 behavioural traits, such as vocal dialects, can be easily quantified, *O. orca* 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). The evidence we provide for *O. orca* suggests that culture and behavioural traditions could have far greater evolutionary consequences than previously assumed (see also Heimlich & Boran, 1999; Baird, 2000). Following the example of Danchin & Wagner (2010), we there-

fore propose that the cultural component of behaviour 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.

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. Gavrillets *et al.*, 2007; Sadedin *et al.*, 2009). Future research on *O. orca* could – to the extent that this is possible with field studies on such a large marine organism – specifically test some of these models and their predictions.

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