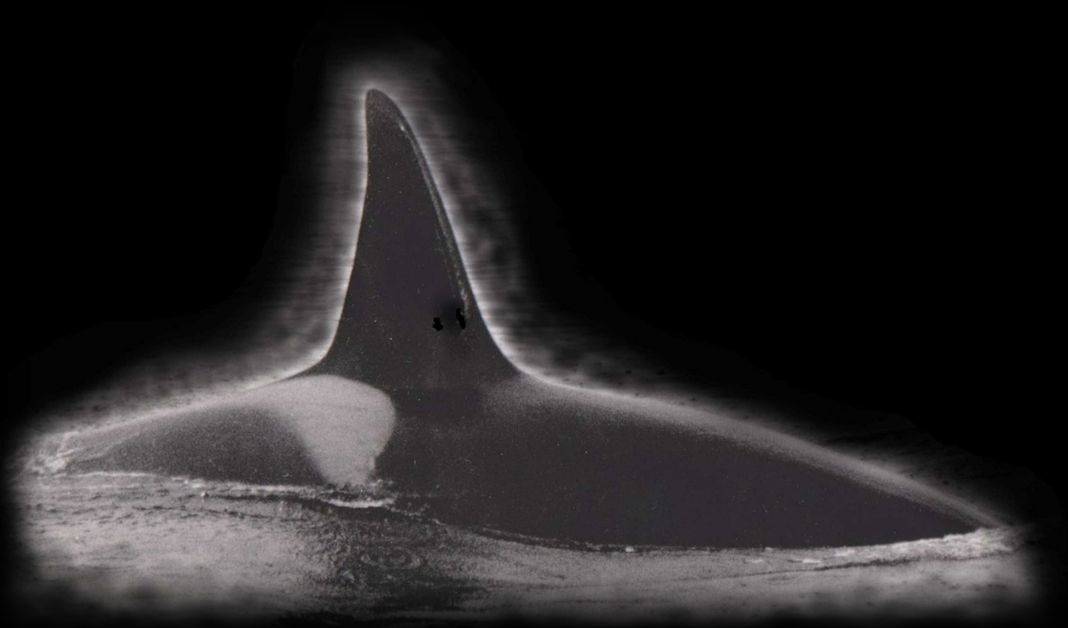

Geographic variation in killer whale colour patterns

Pirjo Mäkeläinen

Helsinki 2020

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Doctoral dissertation, to be presented for public discussion with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki in the Auditorium 1041, Biocenter 2, Viikinkaari 5, on 2nd October 2020 at 12 o'clock noon.

Helsinki 2020

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Luonnonvaraisten eliöiden tutkimuksen tohtoriohjelma (LUOVA)

The Faculty of Biological and Environmental Sciences uses the Urkund system to examine all doctoral dissertations.

ISBN 978-951-51-6131-4 (print)
ISBN 978-951-51-6132-1 (pdf)

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This thesis is based on following papers, which are referred to in the text by their Roman numerals.

I Visser, I. and Mäkeläinen, P. 2000. Variation in eye-patch shape of killer whales (*Orcinus orca*) in New Zealand waters. Marine Mammal Science 16(2):459-469.

II Mäkeläinen, P., van Ginneken, A. and Pietiäinen, H. 2013. Fluctuating asymmetry in the saddle patch shape of the Pacific Ocean killer whale (*Orcinus orca*) populations. Annales Zoollogici Fennici 50: 347-355.

III Mäkeläinen, P., Esteban, R., Foote, A., Kuningas, S., Nielsen, J., Samarra, F., Similä, T., Van Geel, N. and Víkingsson, G. 2014. A comparison of pigmentation features among North Atlantic killer whale *(Orcinus orca*) populations. Journal of the Marine Biological Association of the United Kingdom. Doi: 10.1017/S0025315414000277.

IV Mäkeläinen, P., Visser, I. and Cusson, M. *Manuscript*. Worldwide variation in shape, size and pigmentation of killer whale (*Orcinus orca*) saddle patches.

Contributions

	I	II	III	IV
Original idea	IV,PM	PM	PM,AF	PM
Data Collection	IV	KB, GE, JF, LB-L, NB, AS-J, AB,AVG	PM, RE, AF, SK, JN, FS, TS, NVG,GV	KB, GE, JF, LBL, CM, TS, SK, AB, NB, AS-J, CG, RB, HS, GF, SF, TSH, CMF,IV
Analysis	IV,PM	PM,AVG,HP	PM	PM,MC
Manuscript	IV,PM	PM	PM,AF	PM,IV

PM=Pirjo Mäkeläinen, IV= Ingrid Visser, KB= Ken Balcomb, GE= Graeme Ellis, JF= John Ford, LB-L= Lance Barrett-Lennard, NB= Nancy Black, AS-J= Alisa Schulman-Janiger, AB= Alexander Burdin, RE= Ruth Esteban, AF= Andy Foote, SK= Sanna Kuningas, JN=Julius Nielsen, FS= Filipa Samarra, TS= Tiu Similä, NVG= Nienke Van Geel, GV= Gisli Vikingsson, CM= Craig Matkin, CG= Christophe Guinet, RB= Robin Baird, HS= Hal Sato, GF= Gretchen Freund, SF= Steve Ferguson, TSH= Tatiana Shulezhko, HP= Hannu Pietiäinen, AVG= Astrid van Ginneken, CMF = Chris and Monique Fallows

Abstract

The killer whale (*Orcinus orca*) is an elegantly patterned top predator, which is the largest species in the dolphin family. Great climatic changes and oscillations in weather conditions in the past have influenced many dolphin species. They have needed to adapt and disperse to new and changing environments. Diversification of the species has led to polymorphism and made the taxonomy of many dolphin species challenging. There are also great differences and specialization within the killer whale species, but no subspecies have been accepted yet.

I have focused on variation in colour patterns and colouration in populations around the world, mainly in saddle patch and eye patch patterns. We have showed that killer whale eye patch shapes remain constant over time and that they are a great additional tool for identification. Eye patch size and orientation can also be population specific. I also studied the symmetry of the colouration and possible effects causing fluctuating asymmetry in killer whales saddle patch pattern in North Pacific Ocean populations. When normally symmetrical features develop asymmetrically in nature, there is often some environmental or genetic stress causing it. Some individuals with good fitness can resist that stress, but those who cannot resist it may show causing asymmetry in normally symmetrical features. The southern resident population had much more fluctuating asymmetry in their saddle patch pattern than the other populations. Although transient killer whales are the most contaminated of the populations they were still quite symmetrical. Low genetic variability and small population size may be the reasons for southern resident asymmetries.

North Atlantic killer whale populations are somewhat specialized, but there were not great differences in their saddle patch pattern. It may be due to their recent diversification. A group of killer whales were observed off the west coast of Scotland, that all had slanting eye patches. These eye patches differed from other North Atlantic eye patches as well from all others around the world. Saddle patches were studied in the North Atlantic Ocean, North and mid Pacific Ocean and southern hemisphere oceans. There were no significant differences in variation between these basins. The smooth type saddle patch, where there is no pattern, was the most common and sometimes the only type of patch in some of the studied groups. The Pacific resident ecotype whales had the most variable saddle patches.

We also found differences in saddle patch sizes, the narrowest saddles belonging to the coastal New Zealand population. There is also a variation in saddle patch colouration. No dark saddles were found on the Atlantic side, so the dark colouration seems to be typical to tropical mid and south Pacific killer whales. Variable colour patterns between populations could be indication of differentiation within species. If multiple species of killer whales would be accepted in future, some of these colour pattern features could be recognized as species specific.

Contents

1 Introduction

1.1 Geographic variation

Geographic variation has been an early interest of evolutionary biologists (Futuyma 2013). There is extensive evidence that isolating barriers tend to evolve between geographically distant populations of a species in nature (Ridley 2004). Geographic variation consists of differences among populations of individuals across the geographic range of that species. Variation is maintained by environmental and genetic factors. Olvido and Musseau (2012) divide these factors to random effects and non-random effects. Random effects arise as a function of population size, mutation rates, demography and proximity to other populations. Non-random effects arise from natural and sexual selection. Random genetic drift and chance is known to have greater effect on small populations by promoting the loss of genetic variation. Selection as a non-random effect has less effect in small populations.

Whale populations can have great differences within species in morphology (dorsal fin shape, number of teeth, number of vertebrae, skull features), body size, acoustics, behaviour and colouration (Perrin 2002a). In toothed whales, body size tends to be larger in open waters than in closed seas like in short-beaked common dolphins (*Delphinus delphis*) from North Atlantic, intermediate size in Mediterranean and smallest in Black Sea. Bottlenose dolphin has the same trend being largest in open Atlantic and smallest in Black Sea. There are also size differences between coastal and offshore forms in body size in several dolphin species (Perrin 2002b). Some species have it reversed like in genus Stenella, which have larger coastal forms and smaller offshore forms (Perrin 2002b). In killer whales the Pacific offshore type is estimated having smaller body size than the resident and transient types (Ford et al 2000). In the Pacific Northwest different killer whale ecotypes can be distinguished from their dorsal fin shapes, especially in adult females. Fin types can be more or less curved and the tips of the fins continuously rounded, rounded with a sharper angle or pointed, depending of the ecotype (Ford et al. 2000). Antarctic killer whale ecotypes differ in body size, size and orientation of the eye patch, colouration and presence of dorsal cape colouration (Pitman and Ensor 2003). When groups differ from each other geographically, the different populations can be recognized as subspecies, races, geographic forms or variants (Perrin 2002b).

Killer whales are distributed extremely widely around the world's oceans. Populations have adapted to different conditions and different variants have evolved. This kind of great variation seems to be typical among many dolphin species, including the killer whale. Great diversity within species makes it fascinating to study the differences. In an early study of killer whale colour pattern, fourteen colour components were examined and six of them were found to be geographically variable. Saddle patch and eye patch were among the variable ones (Evans et al. 1982). Evans et al. found the most pronounced differences between groups of northern and southern hemispheres. Evans et al (1982) described three different saddle patch types, only one of which was found in the southern hemisphere.

Despite all morphological variation that has been found between different ecotypes and populations, worldwide mtDNA diversity of the killer whale is low. This kind of low level diversity has been found to be common among species that have gone through a bottleneck situation that has been estimated to have happened during glacial terminations 130 000-140 000 BP (Hoelzel et al. 2002). Reductions and collapsing in important upwelling currents (during the last glacial maxima) in the Northern Hemisphere were assumed to lower production in whole ecosystem and have a declining effect on killer whale populations (Moura et al 2014). They assumed that the only working upwelling system at that time was the Benguela off South Africa. That was supposed to be a refuge for the remaining killer whales. In addition, the waters around New Zealand and Eastern South America may have also served as refuges. That was explained by the high levels of diversity found in the South African population which had 3-4 times higher gene diversity than in the Antarctica (Moura et al. 2014). However, greater genetic diversity may show in less variable saddle patch pattern in killer whales. Barrett-Lennard (2000) found out that transient type whales have significantly greater gene diversity than resident type whales. Transients have mainly two types of saddle pattern (smooth and bump), and there is no pattern on the grey area. Residents with lower gene diversity had a greater variety of patterns on the saddle. Smooth saddle patch pattern was the most common around the world.

1.2 Movements and dispersal

Killer whale is the largest species in the dolphin (Delphinidae) family. Among us humans, killer whales are the most widely distributed mammals around the world. They are more abundant in polar areas and cool waters but can also be found in tropics and subtropics (Rice 1998). Due to the extremely wide distribution, killer whales have evolved and adapted to different conditions and specialized to different prey species (Ford et al. 1998, Jefferson et al. 1991, Pitman and Ensor 2003). Although killer whale populations do not make precise and predictable yearly migrations between feeding and breeding grounds like large baleen whales, they are capable of moving very long distances. They may follow their favourite prey species for a while, wait at their prey's migration route or they may show up in some areas every year if the food is available and abundant. There are great differences of movements between killer whale populations (Matkin et al. 1999, Ford and Ellis 1999, Durban and Pitman 2012, Dahlheim et al. 2008).

Killer whales are known to move up to 160 km per day (Barrett-Lennard 2000). There are differences among individuals, groups and populations in how wide-ranging they are. Some of them move very long distances. Long-distance movements are typical for North Pacific offshore killer whales, moving almost 4500 km between Alaska and California (Dahlheim et al. 2008). Some North Pacific transient type whales were sighted swimming back and forth between Alaska and British Columbia covering around 5000 km (strait measure) of coastline in less than 10 months. They were estimated to have swum about 10 000 km with zigzagging transient swimming style (Ford and Ellis 1999). One male killer whale that was photographed several times in Mexican Pacific waters was also seen in Peruvian waters. The distance between these sightings was at least 5535 km (Guerrero et al. 2005). Researchers deployed a satellite transmitter to one killer whale in high arctic waters and were able to follow its movements for 90 days. That whale swam from northern Baffin Island, past Greenland, Labrador and Newfoundland down to Azores 5400 km (Matthews et al. 2011). Tagged Antarctic B type killer whales swam from the Antarctic Peninsula to subtropical waters off Uruguay and Brazil and back in 42 days, travelling about 9400 km (Durban and Pitman 2012). Killer whales' capability to move long distances and their adaptability has favoured its dispersal around the world and contributed to its development into different ecotypes.

Oceanic environment has much fewer barriers compared to terrestrial habitats, offering great opportunities to mobile species for dispersion. Adapting to the coastal or offshore habitat has created differences between populations in several dolphin species. Morin et al. (2015) have suggested that the rapid global diversification of killer whales as well as bottlenose dolphins in the genus *Tursiops (*Moura et al. 2013*)* commenced during the Pleistocene over 350 000 years ago. During that time fast climatic changes and oscillations were common. New habitats became available in coastal regions and dispersal to pelagic stock and back had an effect of making bottlenose dolphins a polytypic genus (Moura et al. 2013). Past climatic changes have probably had similar effects on other dolphin species including killer whales. Pacific transient clade whales were estimated to have diverged from the other types as early as 700 000 years ago (Morin et al. 2010). They are morphologically and ecologically so distinct, that they were suggested to be an independent species (Baird et al. 1992, Morin et al. 2010).

1.3 Killer whale ecotypes and geographical populations

Dolphins are known to have a great amount of diversity within and among species, which has made their taxonomy complex and challenging (Perrin et al. 2013, Vollmer et al. 2019). It has been noticed that killer whales have a propensity for ecological diversification and to develop quickly reproductive isolation barriers between ecotypes which are maintained even in sympatry (Morin et al. 2015). Morin et al. also estimated that secondary invasions have resulted in sympatry between divergent killer whale lineages. Depending on the methods used it has been suggested that colonization of the North Atlantic by killer whales was followed by a late dispersal event from the North Atlantic back to the North Pacific. However, there are also some indications that dispersal into the North Atlantic has been via the Antarctic (Moura et al. 2015). Cultural traditions and dietary specializations in orca populations seem to be strong reproductive isolation mechanisms (Riesch et al. 2012).

Berzin and Vladimirov (1983) described a new species of smaller size killer whale from Antarctic waters. However, new species or subspecies have not officially accepted or formally proposed even though there is discussion about the differentiated killer whale types in literature (Morin et al. 2010). Currently, the best known ecotypes are three North Pacific ones and three Antarctic + one Sub Antarctic ecotypes. However, there may be more types, depending on how these geographically differentiated populations, ecotypes, subspecies or morphotypes (different types of individuals of the same species in a population) are defined. Word ecotype is described as a phenotypic variant of a species that is associated with a particular type of habitat. Subspecies have different (allopatric or parapatric) geographic distributions (Futuyma 2013). The best known North Pacific populations have been estimated to have differentiated relatively recently during the late Pleistocene and Holocene (Hoelzel et al. 2007). There seems to be some variation in terminology as to what these differentiated killer whale types that are not accepted as subspecies should be called. Ecotypes, the North Pacific ones and the Antarctic ones are well established, but what should the other less differentiated forms which differ from the known ecotypes as well from other populations be called? Perhaps these types could be called pre-ecotypes or orca-types.

There is a map of populations, ecotypes and geographic groups that are used through these studies in manuscript's (IV) Material and methods part.

1.4 North Pacific ecotypes and other Pacific populations

1.4.1 Resident ecotype

In the present situation in the coastal temperate waters in the North Pacific Ocean there are three ecotypes: resident, transient and offshore killer whales (Ford et al. 1994, Ford and Ellis 1999, Matkin et al. 1999). These resident type whales seasonally range from California north, Washington State (USA), through Canadian waters, up to Alaska, eastern Aleutian Islands and the Bering Sea (Matkin et al. 2007), Russian Kamchatka (Burdin et al. 2004) and waters in Northern Japan (Sato 2009). These populations are called: southern residents, northern residents, Southeast Alaskan residents, Kamchatka residents and Japan residents. Resident killer whales eat only fish and at least 22 species of fish or squid are known in their diet. The resident diet is composed mostly of salmon species, the large chinook salmon being the favourite prey (Ford et al. 2000). Residents live in family pods, where offspring of the female stay in the same family group. Also, adult males stay in the same group for life (Ford et al. 2000). Reproduction happens outside the social group during temporary interactions and also from different acoustic clans (Barrett-Lennard 2000). In contrast to that, Ford, M. et al. (2011) found out that in residents many offspring were results of matings within the same 'pod'. However, no evidence was found of matings between close relatives. Resident populations have the most variable saddle patch patterns of all populations (IV). Asymmetrical saddle patches were also more common among residents. From the southern resident population half of the individuals had smaller or bigger asymmetries between the sides. Northern residents had less asymmetry (16%) than southern residents, but they were still more asymmetrical than the studied transients (II). There were 15% asymmetrical saddle patches in the Kamchatkan resident population (II).

1.4.2 Transient ecotype

Transient killer whales (also known as Bigg's killer whales) feed on marine mammals. They are known from southern California up to southeastern Alaska and this group is called West coast community (Ford and Ellis 1999, Black et al. 1997). Transient whales can also be found further up in Alaska, Aleutian and Bering Sea and also in Kamchatka waters (Matkin and Saulitis 1994, Matkin et al. 1999, Burdin et al. 2004, Matkin et al. 2007). There are also transient like killer whales in Japanese waters that feed on marine mammals (Sato 2009). Harbour seals are their favourite prey, followed by harbour porpoises, Dall's porpoises and Steller sea lions (Ford and Ellis 1999). Transient killer whales also eat larger whales, targeting calves and individuals in poor condition. Transients do not necessarily stay their whole life with family members like the residents do. They live in smaller temporary groups and associate more freely with other transients. However there are also strong long them associations among transients, especially with mothers and their offspring. Female offspring disperse more often, while some males still had strong bond with their mothers into adulthood. Some males that disperse their maternal pod become 'roving males' spending time alone or with occasionally associating other groups (Baird and Whitehaed 2000).That kind of fission-fusion society lifestyle is also typical for bottlenose dolphins (Connor et al. 2000). All transient populations had mainly smooth and bump saddle patches, when there is no pattern on the saddle (IV). Asymmetries were also rare in transient saddles. From west coast transients 95% had symmetrical saddle patches and asymmetries were observed only in small details. Californian transients had 99% symmetrical saddle patches (II).

1.4.3 Offshore ecotype

The name offshore population is meant mainly a population identifier, while it is currently unclear if this eastern temperate North Pacific group is an open-ocean population or a continental shelf population (Dahlheim et al. 2008). These third Pacific ecotype killer whales are found in offshore waters near California, Oregon, Washington, British Columbia, Vancouver Island and Queen Charlotte Islands, southeast Alaska and western Alaska. Most sightings are from California, but rarely in summer months. There may be a northward migration during the spring and long-distance movements seem to be their regular behaviour (Dahlheim et al. 2008). Offshore whales feed on fish, Pacific halibut and sleeper sharks are known prey species. Researchers have noted that many offshore individuals have very worn teeth, which is probably due to the rough skin of the sharks. Tooth wear indicates that they eat sharks regularly (Ford, J. et al. 2011, Jones 2006). Genetically offshore killer whales are more closely related to residents than transients. Residents and offshores share more recent ancestors (Barrett-Lennard 2000). Even though residents, transients and offshores are not normally spending any time together (transients avoid residents, Ford and Ellis 1999), in a genetic study one implied mating was found between a transient male and an offshore female (Pilot et al. 2010). Offshore whales had mainly smooth type saddle patches and several notched patterns, which were more common among resident whales. On average there was 91% symmetry between the offshore saddle sides (II, IV).

1.4.4 Eastern tropical Pacific, Hawaii and Mexico

Eastern tropical Pacific (ETP) killer whales inhabit coastal and offshore waters between 30°N to 15°S from Southwest of San Diego, California to Hawaii and down to Peru. These whales do not have a defined ecotype. They are not transients, even though they feed on other whales and dolphins (Olson and Gerrodette 2008). In the study of current and ancestral biogeography, ETP's had haplotypes that fell into clades including the Pacific offshores and transient ecotypes (Morin et al. 2015). Saddle patch variation and colouration of these whales is presented in details in manuscript (IV). About half of these whales (and some Hawaiian and Mexican whales from other sources) have darkish or such dark saddle patches that they are not visible at all. ETP whales which have visible saddle patches were similar to transients, which did not have much pattern variation. All individuals who had a visible saddle patch had the smooth patch, except one individual. Killer whales in Hawaiian waters have been observed harassing some dolphins and feeding on humpback whales and squid (Baird et al. 2006). Those few individuals that were encountered in Hawaiian waters had smooth saddle patches. Killer whales from Mexican waters have been seen attacking marine mammals there (Black et al.1997). Mexican whales have also only smooth saddle patches, except one bump. Roughly half of the ETP whales' saddle patches had darker colouration. There were also dark saddled individuals in Hawaiian and Mexican whales (IV).

1.5 Southern hemisphere

1.5.1 Antarctic and Sub-Antarctic ecotypes

Three different Antarctic and one Sub-Antarctic ecotype have been described in Antarctic waters. Those types are different from the North Pacific ones.

1.5.2 Antarctic A-type

Antarctic A-type killer whales have a large body size and their colouration is similar to that of most killer whales worldwide. There is no dorsal cape pattern. Eye patches are of medium size and parallel in orientation (Pitman and Ensor 2003). A-type killer whales feed mainly on Antarctic minke whales (Pitman and Durban 2012). There is a great size difference between the A and C-type killer whales. Pitman et al. (2007) estimated that A-type females are 1-2m larger and males 2-3m larger than respective C-type whales. Researchers have estimated that A-type whales also occur in South African waters (Best et al. 2014). Antarctic A-type whales have all five types of saddle patch patterns; however, the smooth type was the most common (IV).

1.5.3 Antarctic B-type

Antarctic B and C-types differ from A type by colouration and being smaller in size. Both types have a dorsal cape pattern (see chapter 1.8 of dorsal cape pattern) and their colouration is yellowish grey due to the heavy diatom concentration. B-type killer whales have a very large eye patch (Pitman and Ensor 2003). The B type exists in two different sizes, large (B1) and smaller (B1) size and they have specialized in different prey species. Large B types feed on seals and smaller B-type individuals on penguins (Pitman and Durban 2012). Tagged B-type whales that were followed by satellite telemetry made a rapid migration trip to the tropics, swimming from the Antarctic Peninsula to Uruguay and Brazil and back again, in total 9400km. Researchers suggested that the purpose of this trip was maintenance, allowing faster skin regeneration in warm water (Durban and Pitman 2012). In genetic studies both Antarctic B and C types show signs of recent relatedness, the B1 and B2 populations being the most recently diverged partially sympatric ecotypes (Foote et al. 2016). The B-type population seems to have less variable saddle patches than A and C types, having only smooth type patches and just one individual with a bump type saddle. No notches and hook patterns were found among them (IV).

1.5.4 Antarctic C-type

Antarctic C-type whales are smaller than the B type whales (Pitman et al. 2007). They have a dorsal cape pattern and yellowish grey colouration. The eye patches of C-type whales are small and they have an angular orientation (Pitman and Ensor 2003, I). C-type whales feed on fish, mainly Antarctic toothfish (Pitman and Ensor 2003). C-type killer whales have also been encountered in New Zealand waters, which makes a rather long migration trip from the Ross Sea (Eisert et al. 2015). Antarctic C types have all five pattern types among them, having more patterned patches (notches and hooks) than Antarctic B and A types. The smooth patch type was still most common in this population (IV).

1.5.5 Sub-Antarctic D-type

There is actually a fourth type of killer whale, D type, which lives in circumpolar Sub-Antarctic waters between latitudes 40°S and 60°S. These whales, even adults, have a bulbous head which makes them look like calves (Pitman et al. 2011). These baby face killer whales also have very small eye patches. Their eye patches are the smallest of all ecotypes that I have seen. We recognized these different looking killer whales for the first time when comparing eye patches from local New Zealand killer whales and old pictures from individuals which had stranded in 1955 (I). A few of these stranded individuals, which had eye patches photographed, had very small eye patches with irregular borders. These D-type whales have been estimated to have diverged from the most recent common ancestor as early as 390,000 years ago. The D type has been suggested to be a potential distinct subspecies or even a new species of killer whale (Foote et al. 2013). The saddle patches of the D type are mainly the smooth type. There are just two individuals with bump and one with vertical notch saddle patches (IV).

1.6 Other Southern hemisphere populations

1.6.1 South Africa

Researchers have assumed that in South African waters most killer whales are of the Antarctic A type. However, they have recorded another type, called the flat toothed type. These flat toothed individuals are 1-1,5m smaller than A-type whales, but their flippers are longer and wider and dorsal fins higher than in Antarctic A-type killer whales. Flat toothed individuals had worn teeth, which is most likely caused by a shark-based diet like in North Pacific offshore killer whales. Flat toothed individuals do not have the dorsal cape pattern, that the Antarctic B and C types have (Best et al. 2014). Those killer whales from South African waters whose saddle patches were studied (without knowing the type of the whales), had mainly smooth patches, few bumps and one individual with a vertical notch (IV).

1.6.2 Crozet and Kerguelen Islands

Crozet and Kerguelen Islands waters are visited by three morphotypes (Tixier et al. 2014) of killer whales. Local Crozet Island killer whales are closer to the Antarctic A-type whales. They are generalist feeders, preying on pinnipeds, seabirds, fish and whales. Antarctic C type individuals have visited Kerguelen inshore waters and D-type killer whales are met only in the offshore waters (Guinet 1992, Tixier et al. 2014). Local Crozet Island and D-type killer whales have been reported depredating on the long line fisheries there (Tixier et al. 2016). Local Crozet Island whales have mainly smooth type saddle patches, some bumps and two individuals with vertical notches (IV). Their dorsal fins are clearly chunky and sturdy compared to D types which have slender and sharper dorsal fins. These dorsal fin differences can be seen in the catalogues (Tixier et al. 2009, Tixier et al. 2014).

1.6.3 New Zealand

In coastal New Zealand waters, killer whales feed on short- and long-tail stingrays and eagle rays. This benthic foraging typically happens in shallow waters. When foraging on the bottom they stir up sediment and even dig out the rays from the mud. After hunting they can be seen surfacing with muddy faces (Visser 1999a). There are also sightings of orcas attacking several species of dolphins and having predatory interactions with sperm whales and humpback whales (Visser 1999b). Saddle patches of coastal New Zealand killer whales are mainly smooth, but also some bump and horizontal notches were found. No dark or darkish coloured individuals were observed. More detailed information of the New Zealand whales' eye patches can be found in paper (I).

1.6.4 Papua New Guinea

Killer whales are encountered in Papua New Guinean (PNG) waters almost every year. Most sightings are from April and July, while no sightings were made in January or February. PNG whales feed on scalloped-hammerhead sharks, grey reef sharks, manta rays, blue-spotted rays, yellow-fin tuna, big-eye tuna, Indo-Pacific sailfish and sunfish (Visser and Bonoccorso 2003). All PNG killer whales had smooth type saddle patches. Roughly estimating 70% of the individuals had darkish or dark saddles (IV).

1.6.5 Australia

Over the years there have been sporadic killer whale sightings in Australian waters. The ecology of these whales is not well known. There may be some local populations roaming over wide areas or also migrants from Antarctic or sub Antarctic waters. Those few individuals that we were able to get to our saddle patch study, all had smooth saddle patches. All individuals had also normal light colouration; no dark saddles were found (IV).

1.6.6 Argentina, northern Patagonia

South American sea lions and southern elephant seals appear to be the main prey species of Argentinian killer whales. Killer whale sightings in northern Patagonia, Argentina correlate with the sea lions and elephant seals' breeding cycle and movements (Iñíguez 2001). Some individuals have learned to beach themselves when capturing seal pups from the beach, while others stay in deeper water preventing seals from escaping in that direction. Immature whales practice this beaching behaviour with mature individuals (Lopez and Lopez 1985). Saddle patches from these Argentinian killer whales were all the smooth type, except one bump (IV).

1.6.7 Chilean Patagonia

In Chilean Patagonia**,** killer whales were reported hunting and feeding on South American sea lions, southern fur seals, Magellan penguins, and some gull species and attacking a sei whale. Although humpback whales are abundant in that area, no attacks have been seen (Häussermann et al. 2013). Häussermann et al. assumed that there could be 2 ecotypes inhabiting that area, mammal-eaters and fish-eaters, while local fishermen have observed killer whales removing fish from the lines. It has also been suspected, that Chilean killer whales are feeding on both mammals and fish. There are mainly smooth saddle patches in this population, few bumps and one horizontal notch (IV).

1.6.8 Fiji

Five killer whale individuals have been photographed in waters off Fiji. All of them were so dark coloured that their saddle patches were not visible. One of them had its eye patch photographed and it was white in colour and parallel in orientation (IV).

1.7 North Atlantic Ocean

1.7.1 Norway and Iceland

Northeast Atlantic killer whales feed mainly on herring and mackerel. During a 20-year-study period, no evidence of movements between Norwegian and Icelandic herring feeding populations was found. Some populations were assumed to be more generalist, while some movements and connections were noted around seal predating whales around the Northern Scottish Isles and with Icelandic herring feeders (Foote 2010). Two different types of killer whales have been described in the North Atlantic (Foote et al. 2009). Type 1 whales are found from Norway to Newfoundland including the Norwegian and Icelandic herring feeders and mackerel feeders from the North Sea. They are smaller in size and have been suggested to be generalist in feeding habits. Type 1 whales also have a variable degree of apical tooth wear. Type 2 whales are larger in size, and they have been assumed to be highly specialized feeding on other whales. The teeth of these type 2 whales have been in better shape than in type 1 whales. Type 2 whales were sampled from Scotland and the Faeroe Islands (Foote et al. 2009). These type 1 and 2 type killer whales are not the same as resident and transient ecotypes in the North Pacific Ocean, even if there is a mammal/fish feeding difference. Classification of the Atlantic killer whales to these type 1 and type 2 whales may need to be re-evaluated, while there may be marine mammal feeding specialists as well as generalists feeding on both mammals and fish, but also specialization among fish feeders. Apical tooth wear has been mentioned as being typical for shark feeding killer whales, like offshore types in North Pacific (Ford et al. 2011) and flat toothed individuals in South African waters (Best et al. 2014). Resident and transient whales are mentioned as having teeth in much better condition compared to the offshore whales. Perhaps these Atlantic type 1 teeth samples were from old individuals or there are sharks in these whales' diets. Herring and mackerel diet may not be that hard and abrasive to the teeth as suggested by Foote et al. (2009). There is also specialization among the fish feeders in the Atlantic Ocean. Most of the Norwegian and Icelandic killer whales have smooth saddle patches, however all variants can be found in both of the populations in small amounts (III, IV).

1.7.2 North Sea and UK

Genetic studies in the North Atlantic have found three differentiated populations. The first population (A) consists of herring feeding whales from Norway, Iceland and the North Sea from 60° north. The second population of individuals were from latitudes 66°-51° north from the North Sea and from the west coast of Iceland including samples from UK, Ireland and Iceland. These were mainly mackerel feeders.

1.7.3 Scotland

Seal pup predation has been recorded in Scotland**,** especially during summer months, correlating with harbour seal pupping season. There was a small increase in sightings in December during the grey seal pupping season (Bolt et al. 2009). However, it is not known if these whales have specialized only on marine mammal diet, or whether they are generalists feeding also on fish outside the seal pupping seasons or if they are type 2 whales described earlier. There have also been a few sightings of Norwegian coast killer whales chasing or harassing harbour seals. Finally 13 individuals were identified as specialized on a seal diet, belonging to four stable units. They were reported having erratic swimming patterns, occurring in shallow waters and having a small group size, which is typical to seal eaters. North-south movements were also observed to be timed with seal pupping and weaning seasons. As an interesting detail a few of these whales were observed feeding on herring and seals in 1991. However, they were never seen in the Tysfjord area (between 1986 and 2003) which was a former herring wintering ground nor in the new wintering ground off the Troms and Andfjord areas 2010-2016 (Jourdain et al. 2017). Killer whales from the British waters (without sorting fish/seal feeders) had mainly smooth saddle patches and few bumps and notches. These North Atlantic populations seem to have similar pattern variations, which we assumed to be due to common ancestry (III, IV).

1.7.4 Gibraltar and the Canary Islands

Population (C) were tuna feeders from Gibraltar and the Canary Islands (Foote et al. 2011). These tuna feeders have been observed to push tunas beyond their limits to exhaust them and then capture them. With this endurance-exhaustion technique whales were able to catch small to medium sized bluefin tuna (Guinet et al. 2007). Since the 1980s there has been a dramatic decline of eastern tuna stocks, mostly due to overfishing. Killer whales have learned to depredate on drop-line fisheries, but the low tuna abundance has had effects on this small population and especially the survival rate of calves has declined (Esteban et al. 2016). Spanish killer whales seemed to be smaller in size; the average total lengths (from captured or stranded individuals) were 5,3m for females and 6m for males (Esteban et al. 2016). Killer whales in Spanish waters have only smooth type saddle patches and few bumps, and no saddles with pattern variants (III, IV).

1.7.5 Greenland

There are more observations of killer whales in the western coastal waters of Greenland during the summer months than in winter months. Darkness and ice coverage are probably the reasons for that, even though killer whale movements during the wintertime are not known. They are known to feed on narwhals, beluga whales and several species of seals. Attacks on large whales like humpback whales, minke whales, fin whales and bowhead whales were also reported (Heide-Jørgensen 1988). Examinations of stomach contents have found fish and squid remains in the same stomachs with whale and seal remains, which indicates a more generalist diet at least in some individuals. Mitchell and Reeves (1988) have suggested that there may be a continuous distribution of killer whales between Greenland and Canada. Our sample size from Greenland was small; however, there was some variation in saddle patch patterns. If (smooth and bumps) saddles are combined with pattern-less saddles and (notches and hooks) to patterned, there were 50% pattern less and 50% patterned saddle patches in the Greenland whales (III, IV).

1.7.6 Canadian arctic and Northwest Atlantic

In Canadian arctic and Northwest Atlantic waters killer whales are sighted especially during summer months like in Greenland. These killer whales feed mainly on phocid seals, belugas, narwhals and bowhead whales (Ferguson et al. 2012). Greenlandic and eastern Canadian killer whales have similar feeding habits. It has been suggested that the western North Atlantic killer whales make seasonal north-south migrations. There are sightings from New England, Bahamas, West Indies and also summer records from the Caribbean region (Mitchell and Reeves 1988). Presumably, there are some southward movements by western

Arctic killer whales during wintertime but they are not as predictable as baleen whales. There have also been annual sightings of killer whales off Cape Cod, New England, where killer whales have followed migrating bluefin tuna (Mitchell and Reeves 1988). There were only smooth and bump saddle patches in Canadian arctic killer whales (IV).

1.8 Colouration

Some whale species, like beluga whales (*Delphinapterus leucas*), change their colouration as they age from dark grey to white. Spotted dolphins (genus *Stenella*) are born without spots and spotting develops with age. White-beaked dolphins' (*Lagenorhynchus albirostris*) colour components change while aging, which makes it possible to estimate the maturity of the individuals. All white-beaked dolphin age classes have a light grey eye patch, but their peduncular saddle becomes lighter grey with age, being dark and not visible in juveniles (Bertulli et al. 2016). Grey and partial-grey morphs of southern right whales (*Eubalaena australis*) have been observed to get gradually darker with age (Schaeff et al. 1999). With few exceptions, killer whales are born with main colour patterns like adults. The white parts are at first reddish or yellowish but become white later. When a calf is born it does not have a saddle patch. The saddle patch becomes slightly visible during the first months, becoming clearly visible during the first years. Once the saddle patch has formed, the pattern does not change (Bigg 1982). The development of the symmetrical colouration of the saddle patches can reflect the fitness of the calf and its ability to tolerate stress (II).

Among two populations of southern right whales (*Eubalaena australis*), the inheritance of dorsal skin colour markings has been suggested to be influenced by two genes. The grey-morph and partial-grey-morph phenotypes appear to be controlled by an X-linked gene and the white blaze phenotype by an autosomal gene (Schaeff et al. 1999). In the study of most killer whales colour components, no sexual dimorphism has been observed (Evans et al. 1982). The only area where sexual dimorphism has been observed is the genital area, which was left out from the Evans et al. comparison.

Pilot whales and a few other species among killer whales have a saddle pattern. Mitchell (1970) suggested that saddle pattern is the nearest and simplest version of countershading, which is a primitive and generalized pattern in aquatic environments. Many other dolphin colouration patterns have been explained by camouflage: shading through counter lighting for concealment, camouflage by resemblance to background, disguise through disruptive pigmentation and shadow mimicry (Mitchell 1970). Many whales are mentioned having prominent white colour pattern elements and patches, often bordered with dark pigmentation. These are estimated to function in species recognition or serve to signal the position of school mates in low-light conditions (Perrin 2002a). The rest of the killer whale colouration is bold and bright with contrasting black and white. Herring feeding killer whales in Norway have been observed to turn their white bellies toward the herring school when herding and keeping the fish in a tight formation (Similä and Ugarte 1993). The main black colouration helps killer whales to blend into the dark and murky water when sneaking to attack other types of prey. Other explanation for this kind of predator colouration could be thermoregulation, intraspecific communication, mate recognition, courtship or other social contexts (Endler 1978). The white eye patch may have a function in coordinating behaviour when swimming or resting in line. Eye patch may also reflect light to the eye and help seeing in poor light conditions.

Most of the dolphin species, even those which appear monochrome, have a darker colour pattern starting from the forehead or around the blow hole continuing to the dorsal side behind the dorsal fin. This pattern is called dorsal cape. Killer whales have this pattern while they are fetuses, but it is not expressed in postnatal individuals (Perrin 2002). However, this dorsal cape pattern is visible in Antarctic B type and C type individuals, but not in individuals from other regions (Evans et al. 1982, Visser 1999c, Pitman and Ensor 2003).

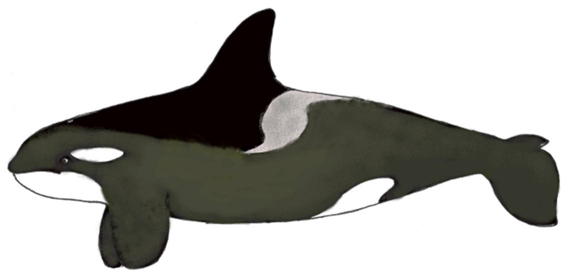

Figure 1. Dorsal cape pattern

2 Methods

2.1 Identification of the killer whale individuals

Considerable progress was achieved in killer whale research, when researchers started to identify individual killer whales in British Columbia and Puget Sound, Washington. They photographed and observed the shape and size of the dorsal fin and nicks and tears in it, as well as the shape of the saddle patch and scars on the saddle and back (Bigg 1982). Saddle patch shapes were noted as being variable from closed (smooth = no pattern) or horizontal tear drop pattern to S- shaped patterns (horizontal and vertical notches and hook). Left and right side saddles were reported as being slightly different in details, but also substantially different saddle patterns were observed in the Pacific Northwest (Bigg 1982).

When being able to identify different individuals from photographs, researchers could follow the individual's life for many years. When the number of identified individuals increased over the years, researchers in the Pacific North West found it harder to identify individuals from both side photographs, so they decided to actively photograph left sides only for identification. Later when other killer whale studies around the world started, identifying individuals from left side photographs became a standard method. However, some populations (Black et al. 1997, Olson and Gerrodette 2008) are also photographed from the right side, but those populations are normally smaller in size.

All of my studies are based on the identification photographs of different populations. When studying the fluctuating asymmetry in six temperate North Pacific populations (II), we used both side photos of the individuals. We compared 512 individuals visually and also measured the degree of asymmetry of 89 southern resident and 55 Californian transient individuals.

From the North Atlantic killer whales we studied saddle patch variation of 975 individuals using also identification pictures (III). In the worldwide variation of killer whale saddle patches (manuscript IV), we studied totally 3179 individuals.

2.2 Challenges in identification

When observing killer whales in the wild, they mostly look the same except the adult males that differ greatly in body and dorsal fin size. Whales come to the surface of the water very briefly to breathe, so the observation and time to take a photo is often very short. However, the variable saddle patch pattern among resident type killer whales in the Pacific Northwest helped researchers to identify different individuals. Individuals with less variable saddles patches without any scars or nicks made the identification harder. When watching photographs from killer whale white eye patches, we realised (I) that those were much more variable than saddle patches. Observing also the differences in the eye patches allowed us to identify some less marked individuals and helped also to identify some whales that were scar less and alike in their saddle patch pattern. Taking photos of the eye patches is more challenging than photographing saddle patches. When a whale's head comes up to the surface, the photographer is almost too late to catch the eye patch. Practicing and knowing whale's behaviour helps as well as good light conditions and calm seas. I have been delighted see that photographing eye patches for identification is becoming more common (Towers et al. 2019).

2.3 Saddle patch shapes

Variation in saddle patch shape was recorded in a few earlier studies (Evans et al. 1982), but Baird and Stacey (1988) described the five variants that become the most useful for categorization of saddle patch variation in populations other than in Pacific waters. Some researchers use the term 'open saddle patch' for the patches that have some pattern on the saddle (Ford et al. 1994), that would be the horizontal and vertical notches and hooked patches. 'Closed' saddles are saddles without any pattern. However, in my opinion this open/close classification is not very convenient.

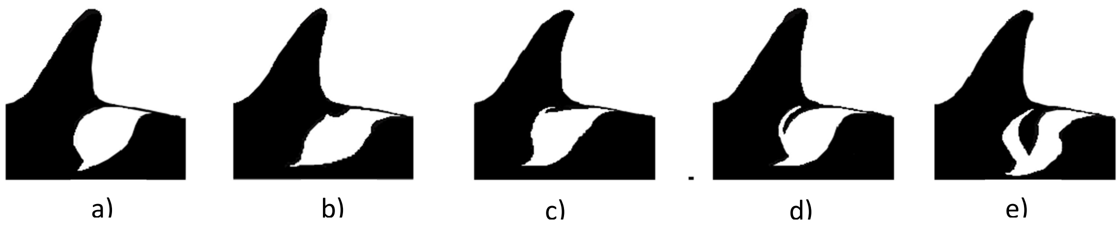

Figure 2. Classifications of the saddle patch shapes based on Baird and Stacey (1988):

a) In the smooth saddle patch, there is no pattern on the grey area.

b) Bump patch has a small corner towards the dorsal fin in the grey area, which creates a round or sometimes less round bump in the upper part of the saddle patch.

c) In a horizontal notch saddle patch, the small black notch intrudes into the grey area in the front part of the patch.

d) A vertical black notch is normally larger than horizontal notches. A vertical notch starts normally from the same area as a horizontal notch and where the bump is located but continues lower. A vertical notch is also located closer to front part of the patch. Sometimes notches can be faint in colouration.

e) In hooked saddle patches, the large pattern is located more in the middle of the patch.

This categorization created by Baird and Stacey (1988) was used throughout my studies. In article (II), six Pacific killer whale populations both side saddles were divided to these five variants. The same categorization was used in article (III) with North Atlantic killer whale saddles. In article (IV) all saddles are also categorized this way. However, we were not able to categorize some saddles, due to the dark colour of the saddle and completely different pigmentation pattern like those on the killer whales in Fiji.

3 Results

In this section I will present my results in greater detail.

3.1 Eye patch shapes

There seems to be great variation in eye patch shapes, especially in small details. Eye patches are also often asymmetrical between sides. We tried to create categories by grouping similar patches together. Most variation was found in front of the eye patch. If the patch was softly curved and had no detail coming out of it, it was categorized as smooth. Patches with hooks coming from the front were placed in the hooked category. Small bumps somewhere in the front of the patch were the bumps category and so on. Eye patch variation from New Zealand waters was presented in chapter I and from the North Atlantic in chapter III.

3.2 Eye patch orientation

In addition to the shape variation the orientation of the patch can be variable. Evans et al. (1982) reported differences in the orientation and position of the eye patch. In the parallel eye patch (Fig. 3 a) the line drawn through the patch ends in the posterior end of the tail stock, while in angular orientation (Fig. 3 b) the front of the patch is located lower than the end and the drawn line ends closer to the dorsal fin. In the third type of orientation, the patch is sloping (Fig. 3 c) so that the front of the patch is higher and the end of the patch slopes downward. The line drawn through the sloping patch ends in whale's ventral area.

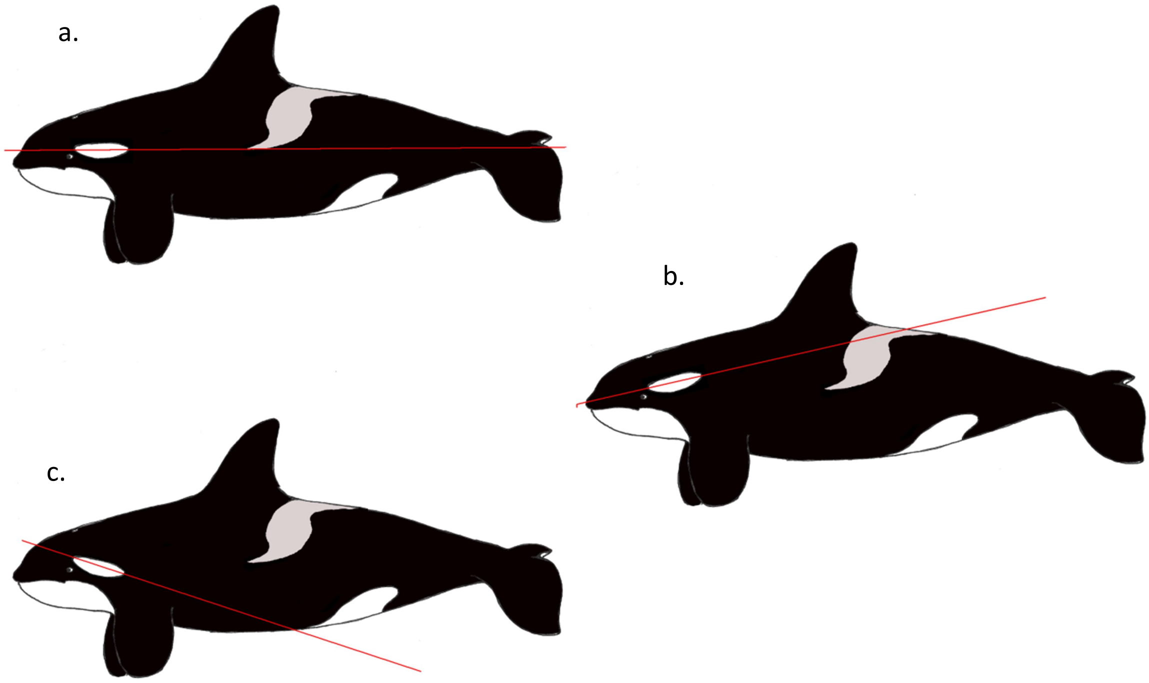

Figure 3. Eye patch orientation a) parallel orientation b) angular orientation c) sloping orientation (Evans et al. 1982, Visser and Mäkeläinen 2000, Mäkeläinen et al. 2014).

Parallel eye patch orientation seems to be the most common around the world. Angular orientation of the eye patch has been reported being population specific to the Antarctic C type whales (Pitman and Ensor 2003). North Atlantic killer whales have mainly parallel orientated eye patches, except one group of 10 individuals off the west coast of Scotland (III). Those were the only sloping eye patches that I have encountered during my killer whale patch studies until recently, when I spotted these few Californian transients with sloping eye patches.

Figure 4. Sloping eye patches of two Californian transient individuals. Most Californian transients have parallel oriented eye patches, except these few individuals. (Photo 2019 Alisa Schulman-Janiger).

3.3 Eye patch size

We estimated the eye patch sizes by creating a ratio measurement of eye patch size and size from the blow hole to front base of the dorsal fin (I). With these ratio measurements we were able find out differences in eye patch sizes between coastal New Zealand and the stranded killer whales, which belonged to the later described sub Antarctic D-type.

3.4 Fluctuating asymmetry and saddle patch pattern

Many population biological, genetic and environmental factors (like unusual temperatures, chemical pollution, lack of food, loss of genetic variation, inbreeding, mutations, bottleneck situation) can increase developmental instability. When an individual cannot resist those effects, normally symmetrical characters may develop fluctuating asymmetry. Heterozygous individuals with greater genetic variability and individuals with better fitness can resist those effects (Møller and Swaddle 1997). Very high levels of PCB concentrations and other persistent toxins were measured from northern and southern resident and transient killer whales in British Columbia, Canada. The transient and the southern residents were considered among the most contaminated cetaceans in the world (Ross et al. 2000). Killer whale calves get their set of toxins already from their mother's milk, which may have an effect on the developing saddle patch pattern's symmetry.

I compared both side saddle patch photographs from six North Pacific Ocean populations: northern residents, southern residents, Kamchatka residents, west coast transients, Californian transients and offshore killer whales. In addition to the visual comparison of all these six populations, we created a measurement method using Adobe Photoshop Elements. Southern resident and Californian transient populations were also compared using this new method (II).

In this measurement method, good quality left and right side photos of each individual were chosen. The left-side photo was coloured blue and right-side red. The right-side photo was flipped horizontally to a mirror image and then the photos were superimposed. The right-side photo was matched to the size of the left side photo. Photos needed to be taken at about same time period, while photos where the individual was of very different age could not be used. After the size match, photos were separated; saddle patches were outlined with a polygonal tool, and then cut out form the photos and pasted onto a new layer and superimposed. Both patches were measured individually, and the measured areas were chosen with a magic wand tool. After superimposing the patches, two areas were identified: total area of patches and area where the patches did not overlap. Numbers of pixels of the selected areas were recorded from the image histogram. The degree of asymmetry was expressed as a pixel ratio of non-overlapping area to total area (II).

As a result of the visual comparison, west coast transients (4% asymmetries) and Californian transients (1% asymmetries) were mainly symmetrical in their saddle patch pattern, even though the west coast transients were the most contaminated population. That contamination was not causing asymmetry to transient populations. All of the fish-eating resident populations had more asymmetrical saddle patches. Northern residents had 17%, Kamchatkan residents 15% asymmetries and from the southern residents almost 50% had more or less asymmetrical saddle patches. Lower genetic diversity and small population size were the most likely the effects causing fluctuating asymmetry in the southern resident population (II).

3.5 Variation of the saddle patch pattern

Variation of the killer whale saddle patch pattern was not as great around the world as I had expected. Hoelzel et al. (2002) have reported of the low genetic diversity of killer whale populations from Atlantic, Pacific and Antarctica. Maybe the low genetic diversity and bottleneck situation which is a severe and temporary reduction in population size (Futuyma 2013) which happened in the past has had some effect on that. Prevalence of the smooth saddle patch in most studied groups was responsible for that. The next four figures show the occurrence of the five saddle patch pattern variants in North Atlantic Ocean, North Pacific Ocean resident and offshore ecotypes, North Pacific Ocean transient ecotype with eastern tropical Pacific, Mexican and Hawaiian and in last figure southern hemisphere saddle patches.

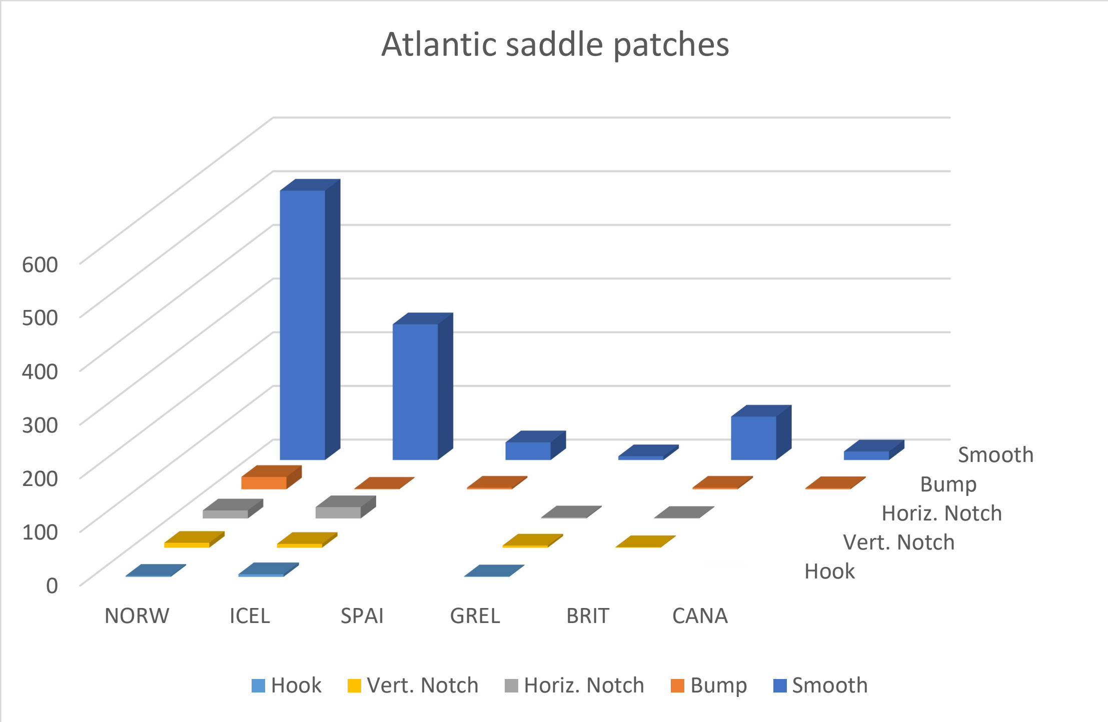

Figure 5. Variation in the killer whale saddle patch pattern in **North Atlantic Ocean**. Studied individuals are from populations from Norway (NORW), Iceland (ICEL), Spain (SPAI), Greenland (GREL), Britain (BRIT) and Canadian arctic (CANA).

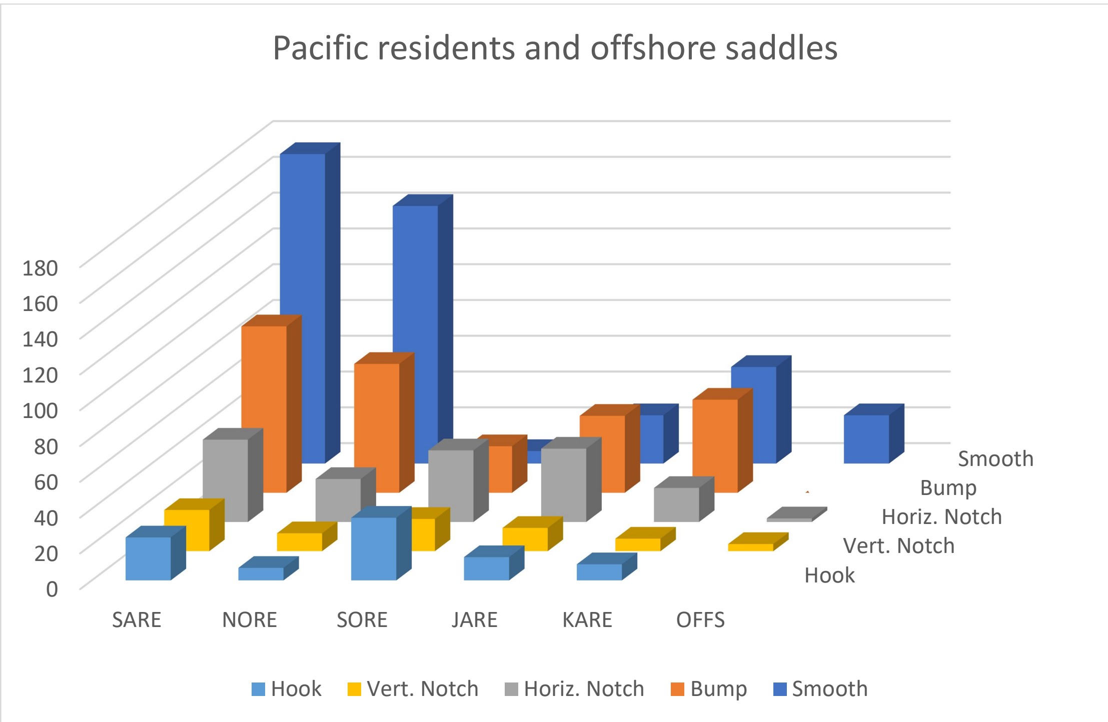

Figure 6. Variation in saddle patch pattern in Pacific Ocean **resident ecotypes and offshore ecotype**. Southern Alaska residents (SARE), northern residents (NORE), southern residents (SORE), Japan reisdents (JARE), Kamchatkan residents (KARE) and offshores (OFFS).

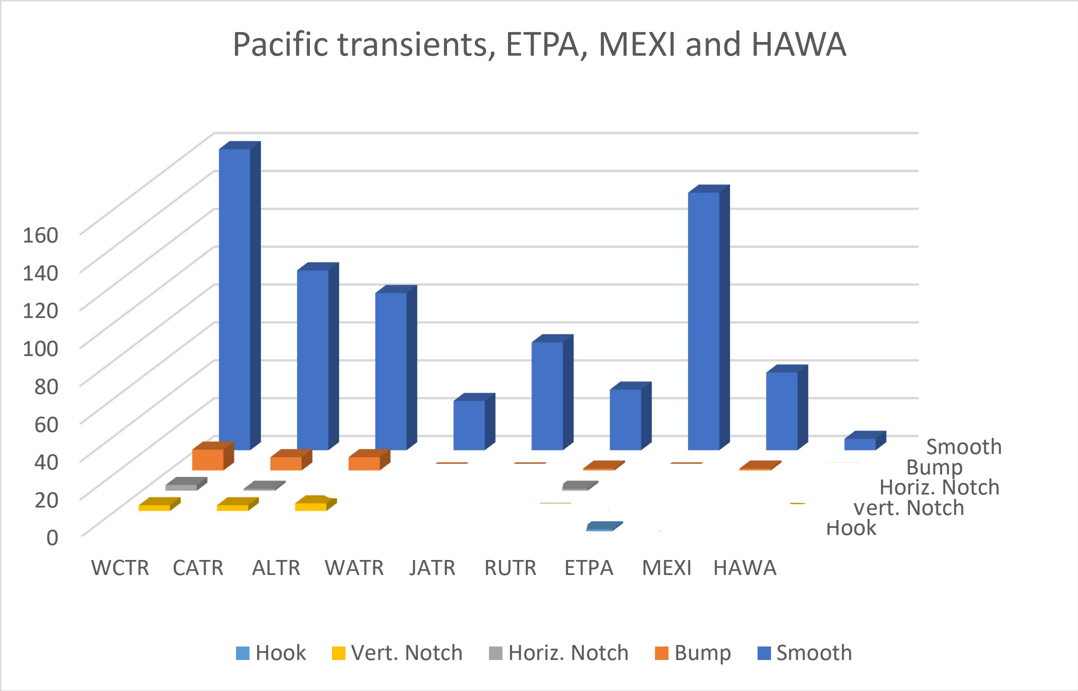

Figure 7. Saddle patch pattern variation in Pacific Ocean **transient ecotype and geographic groups from eastern tropical Pacific, Mexico and Hawaii.** West coast transients (WCTR), Californian transients (CATR), Alaskan transients (ALTR), Western Alaska transients (WATR), Japan transients (JATR), Russian far east transients (RUTR), eastern tropical Pacific (ETPA), Mexico (MEXI) and Hawaii (HAWA).

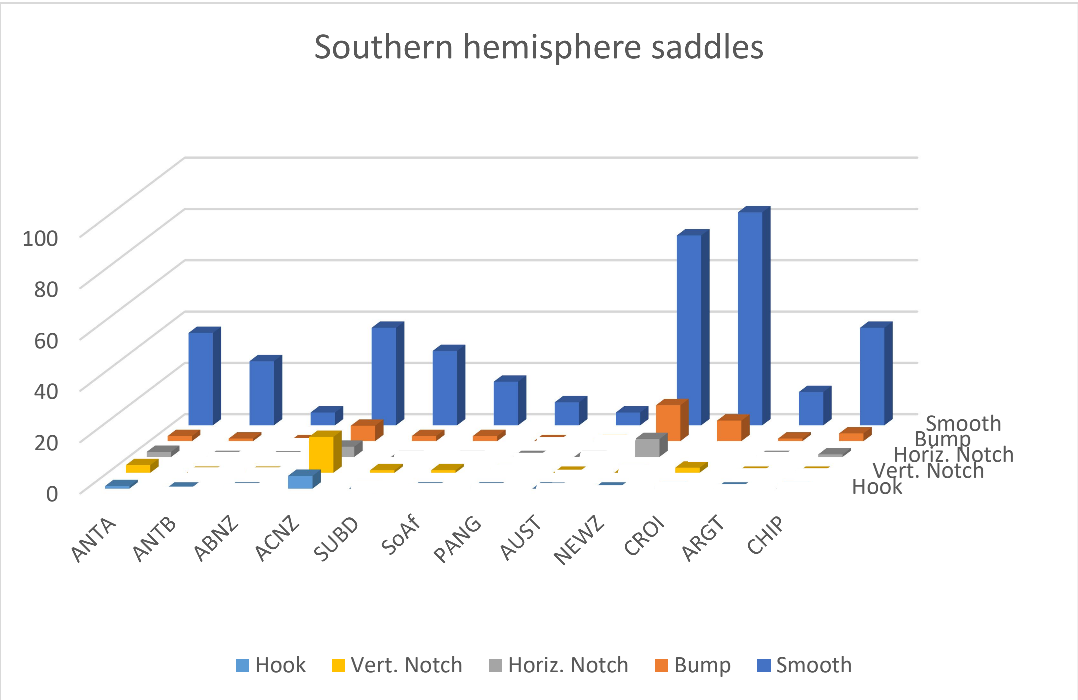

Figure 8. Saddle patch pattern variation in **southern hemisphere geographic groups and Antarctic ecotypes**. Antarctic A-type (ANTA), Antarctic B-type (ANTB), Antarctic B-type in New Zealand waters (ABNZ), Antarctic C-type in New Zealand waters (ACNZ), subantarctic D-type (SUBD), South Africa (SoAf), Papua new Guinea (PANG), Australia (AUST), New Zealand (NEWZ), Crozet Island (CROI), Argentina (ARGT) and Chilean Patagonia (CHIP).

3.6 Saddle patch sizes

Even though killer whale saddle patches have been used successfully in individual identification and photographed intensively, there is not much information of the size of the saddle patches. Transient saddles are mentioned being typically large compared to residents and offshores (Ford et al. 1994). However, no measurements of the saddle patch sizes were available. The other population that stands out with a distinct saddle patch size was the coastal New Zealand population. Some of the New Zealand saddle patches looked very narrow, but not all of them (IV). We wanted to find out if there were any differences in relative saddle patch sizes between geographic groups and ecotypes. We calculated a ratio between the width of the saddle patch and the width of the dorsal fin base measurements (IV). The narrowest and smallest saddle patch dorsal fin ratios were found in New Zealand, Hawaii, Papua New Guinea, Spain and eastern tropical Pacific killer whales. Largest ratios were found in west coast transients, southern residents, Crozet Island, Argentinian and Alaskan transients (IV).

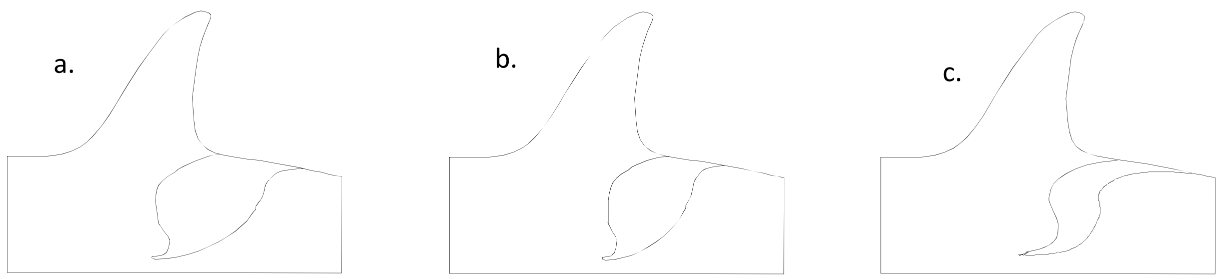

Figure 9. Three saddle patch size variants: a) wide b) medium and c) narrow

Figure 10. Narrow saddle patches of New Zealand killer whales (Photo Ingrid Visser)

Figure 11. Californian transients with wide saddle patches (Photo Alisa Schulman-Janiger).

3.7 Saddle patch colouration

The northern hemisphere killer whale researchers have not really observed the colouration variation of the saddle area, while there is always a clear colour contrast between grey saddle patch and black back. Baird et al. (2006) reported on several dark coloured individuals from Hawaiian waters and later Olsen and Gerrodette (2008) from faint and non-existent saddles from Eastern tropical waters. Some dark individuals can also be found in the Sea of Cortez, Mexico (Black et al. 1997).) No dark individuals have been reported from south Atlantic, so the darker colouration seems to occur in both sides of equatorial Pacific Ocean and southern Pacific. However, there were no darker saddles in New Zealand, Australian and local Crozet Island populations (IV). Perrin (2002a) mentioned that whales in small tanks in captivity can become darker when exposed to the sun. Melanism is known to protect against UV exposure and lower the levels of sunburn lesions (Martinez-Levasseur et al. 2013). They also reported that dark coloured fin whales that stayed in the Gulf of California year-round suffered less from sun and UV originated skin problems than paler migrating blue whales. The darker colour on the saddle patch area is most likely an adaptation to the severe UV rays. However not all the whales were dark coloured in the tropics. In the eastern tropical Pacific population, half of the whales were normally (light) coloured and the other half darkish or dark coloured (IV).

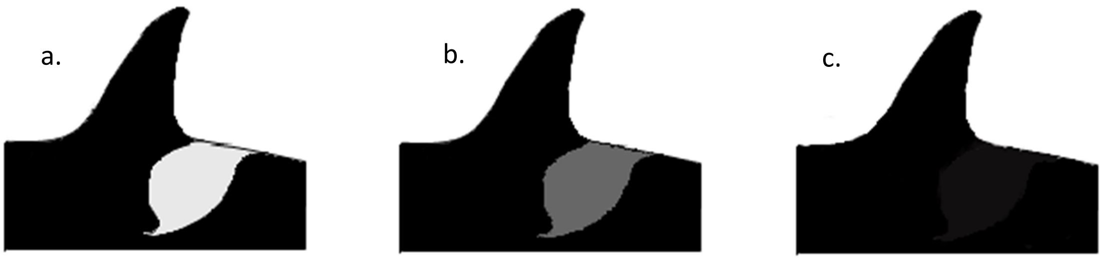

Figure 12. Saddle patch colouration: a) light coloured saddle with good colour contrast, b) darkish/obscured saddle, c) dark/absent saddle.

Figure 13. Obscured/darkish saddled individual (Photo Alisa Schulman-Janiger)

Figure 14. Individual without a visible (dark/absent) saddle patch (Photo Alisa Schulman-Janiger).

4 Discussion

4.1 Speciation

Speciation is the evolution of reproductive isolation between two populations. Reproductive isolation may evolve as a by-product of evolutionary divergence between two populations (Ridley 2004). Whales are capable of moving long distances and an open ocean habitat gives great opportunities for migration. Moura et al. (2014) have suggested that differential habitat use and resource specialization of killer whales have promoted sufficient isolation to allow differential evolution, being also affected by selection and drift. There may also be incomplete speciation in dolphin species, due to the lack of barriers. Populations may have come in contact again, which has led to a complicated taxonomy.

Killer whale distributions are mentioned as being largely driven by prey distribution (Morin et al. 2015). Prey availability may become a limiting factor for these whales with a great appetite and force them to migrate. Specializing in different food sources has most likely reduced competition and promoted the emergence of sympatric ecotypes. Disruptive selection for prey was suggested have resulted the forms of resident and transient types (Baird et al. 1992). They also showed using simple models, that each population's equilibrium density will be higher in the presence of the other type than it would be if there were only one type of killer whale in that area. Stable environment is known to favour specialists and unpredictable and complex environments favour generalists (Clavel et al. 2011). Generalists are also assumed to be more explorative and have higher innovative rates than specialists. One form of behavioural flexibility is innovativeness and propensity to solve new problems. Higher innovation skills may be vital during times of low food availability (Clavel et al. 2011).

Generalist killer whales may, however, have had better chances for survival in new or changing environments, when being more flexible and able to use any available food source. Even though killer whales are mostly specialized to a fish or marine mammal diet, there are also populations or groups that are generalists, like local Crozet Island killer whales (Guinet 1992), some Greenland killer whales (Heide-Jørgensen 1988) and a small group of Norwegian individuals that probably switched from a fish to seal-diet or are generalists (Jourdain et al. 2017). Killer whales in Hawaiian waters appear to be generalists and are likely to be favoured when productivity is low (Baird 2016).

There were great changes in weather conditions in past ice ages, and the effects of melting ice with fresh water entering oceans, raised and lowered sea water levels which opened and closed habitats. These changing conditions forced whales to move and adapt. In allopatric speciation populations that are separated by a physical barrier, which in the whales' world could be inshore/offshore habitat or fresh water/sea water habitat. That kind of barrier reduces gene flow between populations and genetic differences evolve. With time the populations become so different that no gene exchange happens even though the barrier would not restrict the populations anymore. If populations come into contact again, they may become sympatric inhabiting same areas without exchanging genes (Futuyama 2013). In parapatric speciation spatially distinct, adjacent populations, which have some gene flow between them diverge and become reproductively isolated. Range expansion then leads to sympatry (Futuyama 2013).

Sympatric North Pacific ecotype residents and transients occupy the same waters and come into acoustic or visual contact once in a while. Baird et al. (1992) suggested that these two forms of whale are in process of speciation and becoming incipient species. Barrett-Lennard (2000) suggested that their reproductive isolation results from behavioural or social factors rather than physical separation. He also noted that there was a strong behavioural tendency for individuals to avoid associating with killer whales outside their subpopulation. In the study of killer whale's nuclear DNA, data indicated that offshore ecotype whales need to be considered differentiated in sympatry as well (Moura et al. 2015).

There seems to be a lot going on among different killer whale types and with other dolphin species taxonomy as well. It has been suggested that some of the killer whale types are already separate species, like transients (Morin et al. 2010) and Antarctic ecotypes B and C (Pitman and Ensor 2003). However, this theory has not yet been accepted. Taxonomy in Delphinidae family is mentioned as being muddled and vague (Rice 1998) and seems to be challenging for researchers even with the new genetic analysis and methods. There are dolphin species that have a very wide distribution, and different ecotypes have evolved and even speciation has arisen.

Common bottlenose dolphins (*Tursiops truncatus*) have a cosmopolitan distribution in tropical and temperate latitudes. There are inshore and offshore forms, that have clearly differentiated (Hersh and Duffield 1990). Two bottlenose dolphin species were recognised as separate species by genetic differences. However, the Indo-Pacific bottlenose dolphin genetics seems to be twisted, while it may be more closely allied to genus *Stenella* than to genus *Tursiops* (Xiong et al. 2009), genetic data was also found to support one species more: Black Sea bottlenose dolphin (Viaud-Martinez et al. 2008). In the spinner dolphin (*Stenella longirostris*) species there are four subspecies described. This species is described to have more regional variability in form and colour pattern than any other whale species (Perrin et al. 1991). Delphinine genera *Tursiops* and *Stenella* are noted as being paraphyletic and currently there has not been a satisfactory resolution of the phylogenetic relationships in the subfamily (Perrin et al. 2013).

The hump-backed dolphin (genus *Sousa*) species classification was changed from one species to four: Indo-Pacific humpback dolphin, Indian humpback dolphin, Australian humpback dolphin and Atlantic humpback dolphin (Mendez et al. 2013, Jefferson and Rosenbaum 2014). There are differences among these species in dorsal fin shape and size, hump size, skeletal morphology, rostrum shape, molecular genetics, biogeography and colouration.

Early naturalists suggested that there are five species of dolphins in the genus *Sotalia*. For a while all of them were kept as one species tucuxi *(Sotalia fluviatilis)* with two ecotypes or subspecies, the coastal and riverine types. New genetic evidence and morphometric analyses (Caballero et al. 2007) found out that there are two separate species, tucuxi and guiana dolphin (*Sotalia guianensis*), and they have been accepted as separate species.

Common dolphin (*Delphinus sp*.) taxonomy has also been controversial. Although currently there are two accepted species and four subspecies, recent molecular data have challenged this view (Cunha et al. 2015). Genus *Lagenorhynchus* and some relative species have been taxonomically organized to better reflect their evolutionary relationships (by Vollmer et al. 2019).

4.2 Terminology of the different types of killer whales

The killer whale is currently accepted as one species, even though there are great differences between populations. Also, no subspecies have been accepted (Rice 1998) yet. The Society of Marine Mammalogy keeps a list of accepted species and subspecies. Naming the differentiated variants as ecotypes has been successful and widely accepted among killer whale researchers (Riesch et al. 2012, Barrett-Lennard 2011). However, I found it hard to find a word for less differentiated types than ecotypes, but still clearly different forms of killer whales. The word morphotype was used when describing the differentiated sub Antarctic D type killer whales (Pitman et al. 2011, Foote et al. 2013), even though some genetic differences were found, not just morphological differences. Perhaps these differentiated populations could be called pre-ecotypes, before becoming ecotypes or orca-types.

4.3 Differentiation and colouration

Most killer whales have a saddle patch, except dark individuals from the mid and southern Pacific. The smooth saddle patch was the most common patch type around the world, while the other patch types with some pattern on the saddle were common among the resident type whales in the North Pacific including the Kamchatka resident Japan resident like whales. Despite differentiation and specialization among killer whales, their main colouration patterns are not that highly variable. Perhaps the low genetic variability (Hoelzel et al. 2002) among all killer whales explains the prevalence of the smooth saddle patch. Genetically diverse transients had fewer variable saddle patch patterns than less diverse residents. Maybe the original saddle patch for killer whales does not have any pattern on it and patterned patches, notches and hooks are mutations that come up every now and then in small amounts. However, those patches with pattern have become common among the resident type killer whales and show up only in small numbers in other populations. Barrett-Lennard (2000) found that northern resident inferred mating occurred between individuals from different pods within the same community. In contrast to previous studies in different populations, southern resident killer whales' many offspring were the result of mating within the same pod (Ford, M. et al. 2011). Even though breeding happened within the same social group, no mating occurred between close relatives. Small population size, low number of adult males and perhaps similar mate preferences for females may have had an effect that patterned saddle patches have become common in that population. Populations that have more variable saddle patch pattern seem to be more prone to asymmetries in the saddle patch pattern.

Acknowledgements

There was no whale research in my university or nearby when I decided that I wanted to become a whale researcher. Luckily Tiu Similä had started her studies in northern Norway and she came to give a talk in our university. So, thank you Tiu, for taking me along, helping to identify Norwegian individuals and also letting me use the photographic materials. However, it was very difficult to find a subject for my Masters. She recommended I contact Ingrid Visser and then I flew to New Zealand. New Zealand has a huge coastline and finding the whales there was not an easy job, even though Ingrid had created a great system getting information from local boaters if the whales were somewhere to be found. Because the whales were not around at that time Ingrid and I started to look at the pictures of the' kiwi orcas' and compared them to the Norwegian ones, so that's how my patch work started to shape up. Ingrid is an extremely passionate whale researcher, whose enthusiasm with the whales is unique. Thank you, Ingrid for all co-operations, sharing your materials and showing me many New Zealand natural wonders like penguins and possums (if you can't find a whale, you can always find a possum!).

When I was doing my masters, Hannu Pietiäinen agreed to become my supervisor and he proved to be a good one! He has very good knowledge of many species (especially owls), predator/prey interactions and scientific writing. He even agreed to supervise my PhD studies. Thank you Hannu for understanding my not-so-mathematical attitude and guiding me through my both of my theses!

Thank you for all my hydrobiology and aquatic science professors at the University of Helsinki who understood my passion for these whales, Åke Niemi, the late Heikki Salemaa, Jorma Kuparinen and Sakari Kuikka. Thanks, Sakke for the last kick, to get me out of the university! Elina Leskinen and Jorma Kuparinen were my 'seurantaryhmä' which needs to be created for very long-lasting students. They advised me in my final years of studies. Thank you!

I am grateful for so many killer whale researchers around the world, who shared their photo archives and made my studies possible: John Ford, Graeme Ellis, Ken Balcomb, Lance-Barrett-Lennard, Craig Matkin, Astrid van Ginneken, Nancy Black, Alisa Schulman-Janiger, Alexander Burdin, Christophe Guinet, Robin Baird, Hal Sato, Sanna Kuningas, Steve Ferguson, Andy Foote, Ruth Esteban, Filipa Samarra, Nienke Van Geel, Gisli Vikingsson, Renaud de Stephanis, Julius Nielsen, Tatiana Schulezko, Gretchen Freund, Chris and

Monique Fallows…..many more. Thanks to all of my co-authors, especially to Mathieu Cusson for his patience!

Suomalainen Konkordia-liitto gave me a travel grant, which I used to collect materials for these studies. It was especially crucial to my asymmetry study, while it made it possibe to find the 'not existing' right side identification photos in Nanaimo Biological station.

I want to thank Mervi Kunnasranta and Robin Baird for being the pre-examiners of my thesis. Your comments were relevant and helped me to improve this work.

I was never really excited about computers, but all of my skills I have learned from my dear husband Mäxä (also called Kari). He was able to help me with all my technical and practical problems with computers. He also brought several computers back to life, after they died under the huge load of photos. He has also followed me around the world, when I have followed the whales. What a wonderful guy!

Many people have asked me why I started studying whales and why do I have such a weird career and education combination. So, a little background for that: As a child I wanted to have a dog or any pet, but I didn't get one. During my childhood summers at our summer cottage I collected leeches and benthic animals from the lake, observed them and returned them to the lake. My sister and I spent lot of time snorkelling and swimming in the cottage lake. I also loved Jacques Cousteau's underwater films. I thought that it would be nice to do something similar to what Cousteau was doing, but I also had strong feelings that I would like to explore the world. My times at school went smoothly, but we never got homework in the early years (which meant that I hardly ever got or remembered to do the homework later either). I was talented in sports and arts and I also liked woodworking. My awakening for studying at school kind of happened at the last moment and I finished school with good grades. This is a good moment to thank my female classmates for the friendship through the 13 years at school and ever since.

After school, I travelled, tried to get into the university, and failed the exam. However I made it into the flight attendant course. After two years of flying I passed the university entrance exam. I continued flying and started my biology studies. It was a shock to me in the beginning how much reading needed to be done for one credit point (maybe the lack of homework and missing reading routine still affected me). Luckily there was a group of exemplary students, who had done their homework at school. Thank you, Johanna, Milla, Anna-Minna, Maima and Ulla for being such excellent students and friends. During my studies I had a hard time passing the chemistry basics course. When we went on a holiday in Gambia (the chemistry books with me), there was water damage in our bungalow. When we opened the bungalow door in the evening my chemistry books floated out with the water. Studying chemistry was even harder after the trip, because the pages of the books were dried together. However, after learning to study, I was able to finish my master's while on my first maternity leave. This second part of studying has lasted even longer.

My loving parents might have been worried at some point of my life, what will I be, but they encouraged me and kept their positive attitude. My father even paid for me to get a truck driving licence, in case other things didn't work out. My parents have also helped us in many ways, taking care of the kids, when there were some busy times fixing the house, studying and flying. Thank you to my parents Maija and Väinö for everything!

I am happy that our kids are interested in the nature. They have been as excited as I was catching leeches and bugs at the summer cottage. They have also been water monsters since they started baby swimming as infants. Luckily kids inherit genes and skills from both parents, in this case they both have got dad's math skills and they both have learned to do their homework. Thank you, Krista and Noa for being you! Krista's dog Eetu has acted as a mental support study-dog. He took me out for refreshing walks during these last intensive writing episodes.

I would also like to thank my dear sister Misku and her kids Sera and Auro for their company and positive attitude through my almost everlasting studies. Thank you, to my mother-in-law Maire for helping to take care of us and the kids at busy times. Giselle Richards agreed to have a look at my English in this intro part, thank you, Giselle! All my flying co-workers at Finnair have been supportive and very inspired about my whale studies. My present and all earlier volleyball teammates, thanks for playing with me! Playing volleyball keeps things balanced in life. Thanks to all my friends, who may (or not) have believed in me being able to get this almost forever lasting study finished. Then, finally, I would like to reveal my secret things for a happy life: Family, Friends, Whales and Volleyball!

Helsinki, November 2019

Pirjo Mäkeläinen

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